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THE STAGES OF DEVELOPMENT IN THE EMBRYOLOGY OF THE HORNED PASSALUS BEETLE, POPILIUS DISJUNCTUS ILLIGER

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INTRODUCTION

The horned passalus beetle, *Popilius disjunctus* Illiger (the *Passalus cornutus* Fabricius of many authors), possesses many interesting characteristics which make this widespread species especially desirable for developmental studies. One of these advantageous characteristics is the large size of the eggs compared to those of other common insects. When laid, the egg measures 3.0 by 2.4 mm. and when ready to hatch, the egg has increased to 3.7 by 3.2 mm. This large size makes the eggs very easy to manipulate. A second advantageous feature is the fact that the incubation period of sixteen days is long enough to enable the investigator to collect many transition stages in the development of the egg and allows for more convenient and accurate studies than if the embryological course were exceedingly rapid. Lastly, this large beetle completes its whole life history from egg to imago in a single summer, and similarly, this favors developmental studies.

In spite of the obvious advantages, the only developmental studies of passalus have been confined to investigations of the development of the gonads and of the central nervous system. There are several difficulties which may have precluded a more extensive use of this species in embryological studies. One of these is the difficulty and inconvenience in securing eggs of known ages. Oviposition occurs in the field in June and the first half of July, but has not yet been induced in the laboratory at other seasons of the year. In order to obtain a supply of eggs of known ages, it is necessary to bring adult beetles into the laboratory, place them in individual finger bowls with a little moist wood pulp, and examine the bowls at least once each day for the newly laid eggs. Under these conditions females usually lay fewer than six eggs, and after several days cease laying altogether, or lay pale green, small sized eggs which do not develop normally. This fact necessitates replenishing the supply of egg laying females. Since no satisfactory criterion has been observed for distinguishing between the sexes, this

method of obtaining eggs of known ages becomes doubly inconvenient. Finally, it has been observed that even eggs of the same age may show considerable variation in degree of development, so that the use of the age of the egg is often an unsatisfactory criterion for determining the state of development.

Large numbers of eggs of unknown ages in various phases of development can be collected from the tunnels in hardwood logs in the field. Usually the number of eggs in a nest averages between twenty and thirty-five at the height of the egg laying season. However, one nest in Dougherty County, Georgia, yielded eighty-four eggs and sixteen first instar larvae. Collections of fifty or sixty eggs from one nest are not uncommon.

In view of the many desirable features which *Popilius disjunctus* possesses and the difficulty in collecting eggs of known ages, the primary objective of this project is to establish recognizable developmental stages by correlating the age of the embryo with its stage of development. Then the plentiful and easily collected eggs of unknown ages, upon removal of their chorions, can be placed in their proper embryological phases. In this manner the collector can obtain a far greater number of eggs in a given time than by using the previously described method of obtaining eggs of known ages. A second objective is to study the external features of the embryo, and any internal structures that can be observed, to establish general topography and landmarks for further, more detailed embryological investigations. The third objective is to compare certain phases of the embryology of *Popilius disjunctus* Illiger with conditions found in other insects, limiting these observations and discussions, for the present, to only those structures visible with the use of the stereoscopic dissecting microscope of 20X or lower magnification.

HISTORICAL SURVEY

While the literature concerning passalus is rather extensive, developmental and embryological studies are few and fragmentary. Riley (1872, 1873) described the eggs and larvae of passalus and pointed out the rapid completion of the life cycle. Hinds (1901) concluded that it was impossible to distinguish between the sexes of passalus. Ohaus (1900, 1909) contributed much to our knowledge of the social behavior and life histories of several South American passalids. Miller (1931) showed how pupal case building might be observed in the laboratory. Pearse (1936) described the ecology, particularly the food habits and parasites, of the horned passalus. Cody and Gray (1938) traced the changes in the central nervous system from egg to adult. Gray (1944) studied the changes in water content throughout the life cycle, and (1946) summarized the literature on passalus, as well as making essential contributions to our information regarding the life history of this species. Krause (1946, 1947) described the structure and development of the gonads from the egg to the adult.

In contrast to the paucity of developmental studies on the horned passalus, the literature on the development of other coleopterans, and insects as a group, is voluminous. For this reason, it seems desirable to mention only such standard works as Korschelt and Heider (1899),

Snodgrass (1935), and Johannsen and Butt (1941) which were used as the major sources for the background on the embryology and development of insects in general.

MATERIAL AND METHODS

Eggs of both known and unknown ages were used in this study. The specimens of unknown ages were collected from rotting hardwood logs in sections of Delaware, Georgia, Maryland, and southern Pennsylvania. Eggs of known ages were obtained by collecting adult beetles from the field, placing them in individual finger bowls with a little moist wood pulp from the tunnels, searching the bowls daily for the newly laid eggs, and then incubating the eggs at 28 degrees C. for from one to fifteen days. Newly hatched larvae were obtained by allowing field-collected eggs to hatch in the laboratory.

Both eggs and larvae were fixed in Kahle's fluid, washed in 50% and stored in 70% ethyl alcohol. It was found that the eggs thus treated usually turned a dark green or brownish color, even though the eggs had been red, dark red, or brownish green before fixation.

Prior to the removal of the chorions, the eggs were placed in a dilute solution of commercial sodium hypochlorite for about five minutes, or until the chorions turned tan in color and became noticeably thinner. The eggs were then returned to the alcohol, and the chorions were removed with the aid of fine tipped forceps and under a stereoscopic dissecting microscope.

Some embryos were stained with aqueous alum cochineal, while others were stained in dilute Harris' or Ehrlich's hematoxylin. They were destained in acid alcohol until sufficient contrast between embryo and yolk was obtained. The newly hatched larvae were studied unstained.

After the serosas were removed from the embryos, the various stages were studied and drawn with the aid of a stereoscopic dissecting microscope with 20X magnification. The specimens were not mounted on slides, but were drawn while they were submerged in a little dish of alcohol. This was partially necessitated by the fact that the same specimens were to be used in the preparation of serial sections in future studies, and also by the fact that the objectives of the project were to determine those stages of development and structural landmarks which could be recognized readily with the use of the dissecting microscope or a hand lens.

Embryos of known ages were used as standards for determining the extent of each stage of development. As previously mentioned, there is often a considerable variation in development within a single age group. When such variations in a particular age group were encountered, the most advanced embryo was chosen as being the most probable representative of the group.

Since the number of specimens for each of the sixteen days in the incubation period was not sufficiently large for a satisfactory study, intermediate phases were therefore selected from the plentiful supply of eggs of unknown ages to fill in the gaps and to give a more nearly complete series of embryonic stages.

OBSERVATIONS

Days 1 to 4: During the first four days of embryonic life passalus exhibits no manifestations of development which are visible by examination with the dissecting microscope.

Days 5 and 6: During the fifth day the first evidence of development appears. A ventral plate, or first rudiment of the germ-band, appears as a small, disc-shaped, darkly staining area (Fig. 1), about one-third the distance from the anterior pole of the egg. A little later, in a hematoxylin stained specimen (Fig. 2), the central area of the ventral plate could be seen to be composed of five or six densely staining clumps, the embryonic rudiment, with a lighter staining halo and a dark periphery. Still later the ventral plate appeared roughly pear-shaped in outline, with the broader end directed anteriorly.

During the sixth day of incubation the embryonic rudiment has elongated (Fig. 3) and the embryo can be roughly divided into two regions. The more anterior region is the protocephalon (*pch*) or cephalic lobes, and the posterior region is the protocorm (*pcm*), or remainder of the embryo. A narrow, darkly staining area marks the lateral limits of the embryo, and a wide, darkly-staining band in the midline (*g. b*) extends from nearly the anterior to posterior ends of the ventral plate. The embryo at this phase of development lies on the ventral surface of the anterior half of the egg. Later in the sixth day, the embryo assumes the somewhat hour-glass-shaped outline shown in Fig. 4.

Day 7: During the seventh day of development the embryo undergoes the process of segmentation. The cephalic lobes (Fig. 5, *c. l*) are wider and more sharply defined than the rest of the embryo. Several somites can be seen as darkly-staining blocks in the mid-region of the germ-band. The segments of the thoracic region (*t. s 1–3*) are clearly defined at this stage, but there is merely a hint of segmentation anteriorly and posteriorly. The germ-band area of the protocephalic region and of the extreme caudal aspect remain as yet unsegmented. Segmentation does not appear to involve the surface layer at this stage.

In a short time the embryo has elongated to occupy almost the entire long axis of the egg (Fig. 6). The anterior region is still dominated by the cephalic lobes, with the stomodaeal invagination (*s. i*) having formed in the midline. The posterior terminal region is made up of the anal segment, or telson (*tel*). Between the cephalic lobes and the

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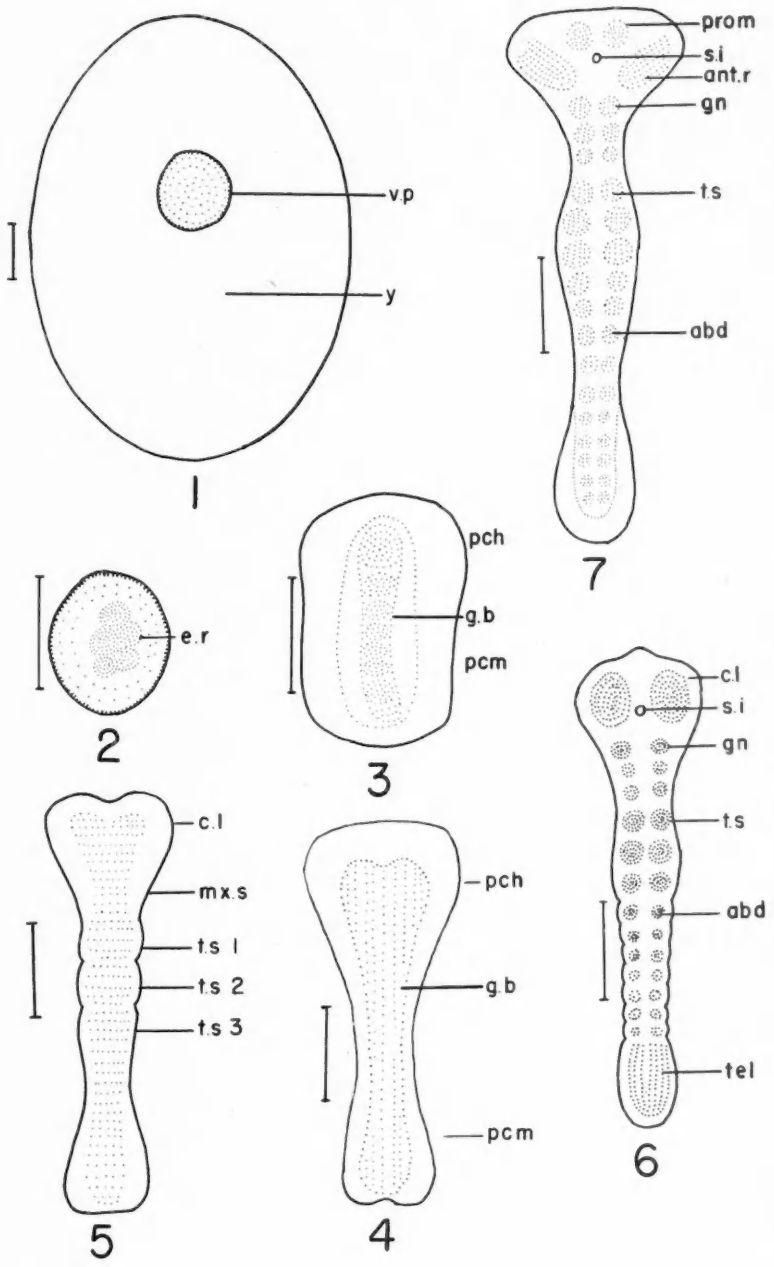
EXPLANATION OF PLATE I

FIG. 1. Ventral view of egg incubated for 5 days. FIG. 2. Ventral plate slightly older than that shown in Fig. 1; hematoxylin stained. FIG. 3. Embryo in sixth day. FIG. 4. Embryo later in sixth day. FIG. 5. Embryo early in seventh day. FIG. 6. Embryo later in seventh day. FIG. 7. Embryo near end of seventh day.

ABBREVIATIONS: *abd*—abdominal somite; *ant. r*—antennal ridge; *c. l*—cephalic lobe; *e. r*—embryonic rudiment; *g. b*—germ band; *gn*—gnathal somite; *mx. s*—maxillary somite; *n. r*—neural ridge; *pch*—protocephalon; *pcm*—protocorm; *prom*—labral prominence; *s. i*—stomodaeal invagination; *t. s*—thoracic somite; *tel*—telson; *v. p*—ventral plate; *y*—yolk.

NOTE: Reference lines equal 0.5 mm.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gn
t.s
abd
tel
6
c.l
mx.s
t.s 1
t.s 2
t.s 3
5
pch
g.b
pcm
4

telson lies the primary trunk region, composed, in the definitive segmented condition, of sixteen somites. These are, namely: three gnathal, three thoracic, and ten abdominal somites. In Figure 6, however, the limits of the more caudal abdominal segments are not clearly defined. The cephalic lobes and the thoracic regions of the embryo are broader than the other parts, and the first eight segments of the primary trunk region (*i.e.*, the gnathal, thoracic and the first two abdominal) have become slightly thinned out on the midline.

At the end of the seventh day (Fig. 7) the definitive number of sixteen somites can be seen in the primary trunk region. At the extreme rostral end two small prominences (*prom*) have arisen, one on each side of the midline. Lateral and caudal to these prominences a pair of somewhat elongate, thickened ridges (*ant. r*) can be seen.

Day 8: Early in the eighth day the embryo has elongated to such an extent that the caudal end lies bent over the posterior pole of the egg. (Figs. 8, 9.) Each of the somites is seen to possess a pair of appendages. The thoracic appendages are larger than the others and project ventrally and caudally. The gnathal and abdominal appendages are quite small, the latter appearing as only slight swellings. The antennae (*ant*) appear as small rounded swellings caudal and lateral to the stomodaeal invagination (*s. i*). The prominences (*prom*) have moved mesially and approximate each other. A double, longitudinally directed thickening (*n. r*) along the midline extends from the antennae almost to the proctodaeum (Fig. 9, *pct*) in the telson. There appear to be slight swellings, the future nerve ganglia, arranged in segmental fashion, with four cephalic, three thoracic, and ten abdominal swellings (Figs. 8, 9). The first cephalic swellings appear larger than the others and have a slightly irregular, ill-defined outline.

Later in the eighth day the rudiments of the head appendages and of the abdominal appendages have developed into paired lobes, all approximately equal in size. The thoracic appendages have undergone the most growth and are larger than any of the other appendages. The paired prominences rostral to the stomodaeum have begun to merge.

Day 9: Early in the ninth day of development (Figs. 10, 11) the paired prominences of the previous stage have fused to form the labrum (*lbr*), which still bears a little furrow on its midline, marking the region of fusion. The head appendages, exclusive of the antennae, show signs of their future lobed condition at their distal ends. At this phase the

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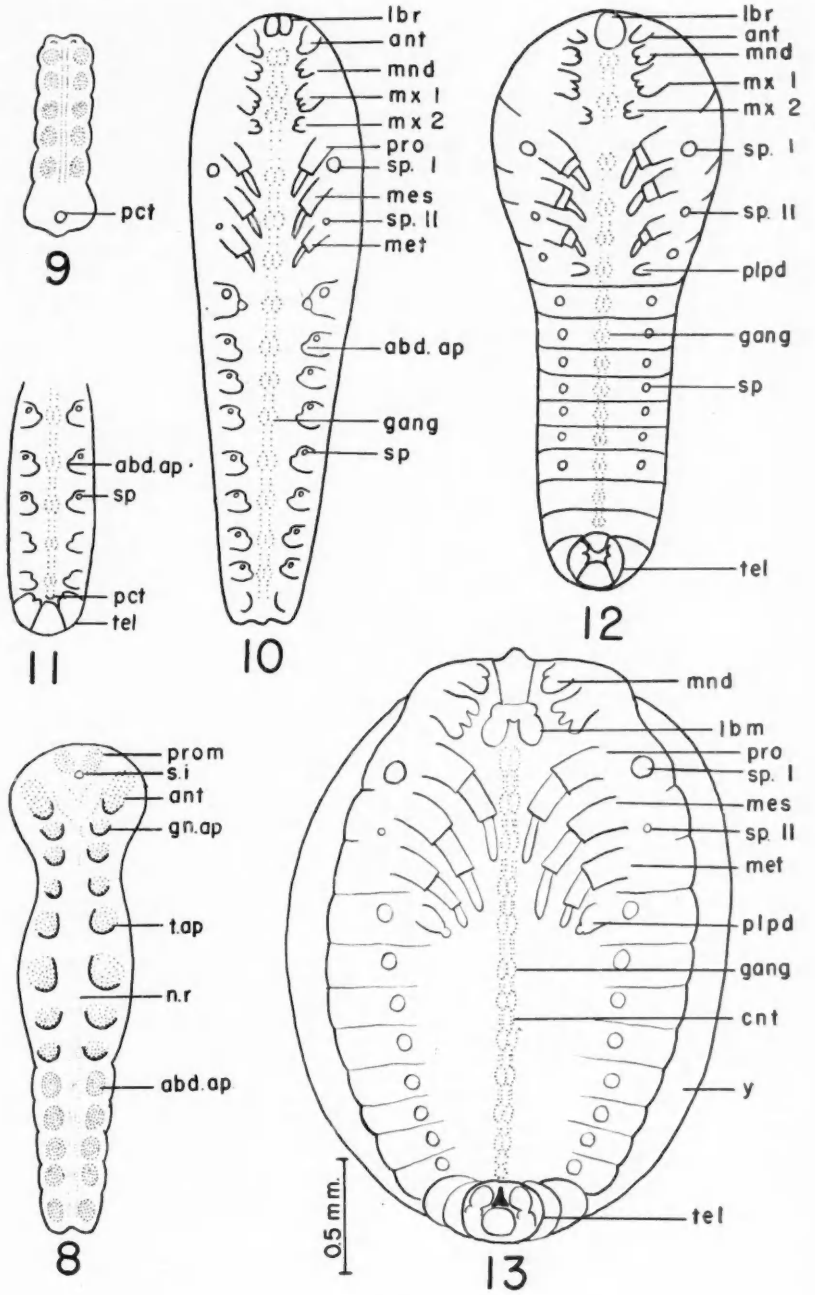
EXPLANATION OF PLATE II

FIG. 8. Embryo of eight days; ventral view of egg. FIG. 9. Embryo of eight days; posterior polar view of egg. FIG. 10. Embryo early in ninth day; ventral view of egg. FIG. 11. Embryo early in ninth day; posterior polar view of egg. FIG. 12. Embryo later in ninth day; ventral view of egg. FIG. 13. Embryo in tenth day; ventral view of egg.

ABBREVIATIONS: *abd. ap*—abdominal appendage; *ant*—antenna; *cnt*—intersegmental connective; *gang*—ganglion; *gn. ap*—gnathal appendage; *lbm*—labium; *lbr*—labrum; *mes*—mesothoracic leg; *met*—metathoracic leg; *mnd*—mandible; *mx 1*—first maxilla; *mx 2*—second maxilla; *n. r.*—neural ridge; *pct*—proctodaeum; *plpd*—pleuropodium; *pro*—prothoracic leg; *prom*—labral prominence; *s. i*—stomodaeal invagination; *sp*—spiracle; *t. ap*—thoracic appendage; *tel*—telson; *y*—yolk.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cnt
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0.5 mm.
13

mandibles (*mnd*) and second maxillae (*mx 2*) appear bilobed, whereas the first maxillae (*mx 1*) appear trilobed.

The three pairs of thoracic legs, which have enlarged over those of the previous stage and are all approximately equal in size, have become divided into two podites, or limb segments. The abdominal appendages (Figs. 10, 11, *abd. ap*) have not enlarged to any great extent and they remain as simple lobes. Caudal to the proctodaeum the telson (Fig. 11, *tel*), or anal segment, now consists of three lobes: a single median caudal lobe and a pair of lateroanterior lobes.

A pair of spiracles (Fig. 10, *sp. 1*) has appeared at the anterior margin of the mesothoracic segment, and a smaller pair has formed at the anterior margin of the metathoracic segment. Paired spiracles are located at the anterior margins of each of the first eight abdominal segments, the spiracles of the first abdominal segment being slightly larger than those of the following seven somites.

In the ventral midline of the embryo the future nerve ganglia are visible, although not clearly defined, and there now appear to be three cephalic, three thoracic and ten abdominal thickenings. The more rostral of the ganglia soon become covered by the developing head and mouthparts, and further observations become impossible.

Later in the ninth day (Fig. 12) the cephalic end of the embryo has begun to develop ventrally and caudally so that the labrum (*lbr*) covers the stomodaeum. In similar fashion, the caudal end has grown ventrally and cephalad so that the telson (*tel*) covers the proctodaeum. The antennae (*ant*), which had been postoral in position in the previous stage, have migrated rostrally and now lie lateral to the covered stomodaeum. The gnathal appendages have not undergone any pronounced change other than a slightly rostral, general shift and a mesial migration of the second maxillae (*mx 2*). The thoracic appendages are seen to be composed of three podites. With the exception of the pleuropodia (*plpd*) on the first abdominal segment, the abdominal appendages have disappeared.

The first pair of thoracic spiracles has shifted from its previous position at the anterior margin of the mesothorax (Fig. 10, *sp 1*) and now lies at the posterior margin of the prothorax (Fig. 12, *sp 1*). The second pair of thoracic spiracles (*sp 11*) remains unchanged in location, but is noticeably smaller in size.

During the end of the ninth day the whole embryo has shifted in position in such a manner that the head of the embryo extends over the anterior pole of the egg. The caudal end, which formerly lay bent around the posterior pole (Figs. 10, 11), now lies almost entirely

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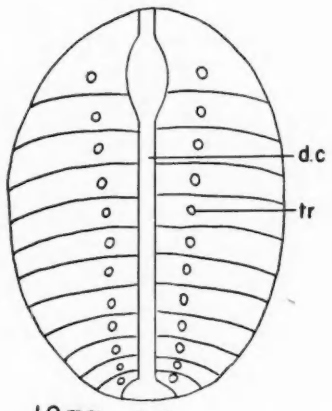
EXPLANATION OF PLATE III

FIG. 14. Embryo in the tenth day, anterior polar view of the egg; same specimen as in Fig. 13. FIG. 15. Embryo early in the twelfth day, ventral view of the egg. FIG. 16. Embryo early in the twelfth day, dorsal view of the egg; same specimen as in Fig. 15. FIG. 17. Embryo later in the twelfth day, viewed from the right side. FIG. 18. Embryo in the fourteenth day, viewed from the original ventral aspect of the egg.

ABBREVIATIONS: *ant*—antenna; *cl*—claw; *d. c*—dorsal closure; *gang*—ganglion; *lbm*—labium; *met*—metathorax; *met. l*—metathoracic leg; *mnd*—mandible; *mx 1*—first maxilla; *plpd*—pleuropodium; *sp*—spiracle; *tr*—trichogen.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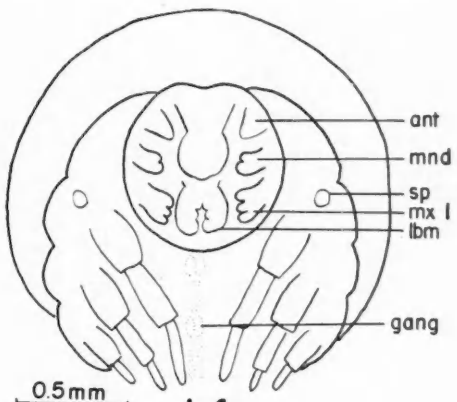
16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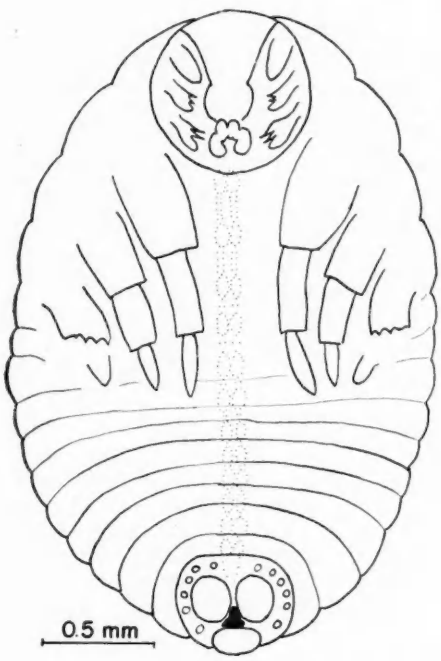
14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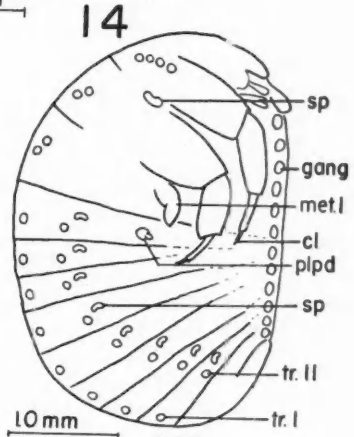
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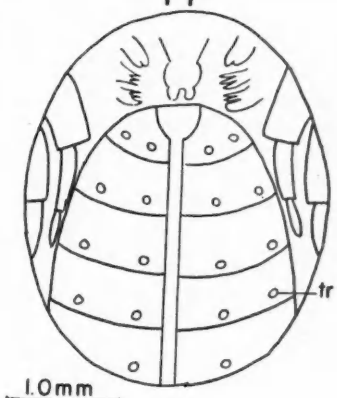
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18

on the ventral aspect of the egg as a result of this forward shift (Fig. 12). The thickenings of the neural ridges have merged to form the clearly visible nerve ganglia (*gang*).

Days 10 and 11: During the tenth day there is a general increase in size and extent of the embryo, with lateral expansion in all regions but the head. In the cephalic area the changes are mainly those of position, with further ventral curvature of the rostral portions. There is also a partial fusion of the last four head appendages, with the second maxillae merging to form the labium (Figs. 13, 14).

The metathoracic legs have not developed as much as the first two pairs, and consequently appear somewhat smaller. The pleuropodia have segmented into two podites, but otherwise appear little changed. The second pair of thoracic spiracles has almost completely disappeared, but the first pair is still clearly visible at the posterior margins of the prothorax. The nerve ganglia (Fig. 13) appear clearly bilobed in the ventral midline and are joined to each other by intersegmental connectives (*cnt*). Early in this stage fourteen ventral ganglia are present: one cephalic, three thoracic, and ten abdominal. Later (Fig. 13), only nine of the abdominal ganglia are visible, the last two having lost their intersegmental connectives and undergone fusion.

In some specimens of the late tenth day the forward shift of the whole embryo has been so great that the telson becomes located well forward of the posterior pole of the egg. But, by the eleventh day, the head has come to occupy the anterior pole of the egg, and the tail region has come to lie at the posterior pole. Dorsal growth of the lateral margins of the embryo continues until about half of the yolk is enclosed. At the end of the eleventh day only a small portion of the yolk remains unenveloped dorsally by the extending body wall.

Days 12 to 14: Early in the twelfth day the dorsal closure of the body wall has been virtually completed (Fig. 16). On the dorsal aspect of the embryo a pair of large, darkly staining clumps, or trichogens (*tr*), can be seen on each segment, slightly lateral to the dorsal closure (*d.c*).

Later in the twelfth day completion of the dorsal closure occurs and the yolk is entirely enveloped. The ventral curvature of the abdomen, along with the growth of the somites, results in the caudal region of the embryo being directed cephalad (Fig. 17). At this phase of development the metathoracic legs have become specialized into small paw-like structures. The prothoracic and mesothoracic legs have developed small claws (Fig. 17, *cl*) at the ends of the third podites.

The ventral nerve chain is now composed of one cephalic, three

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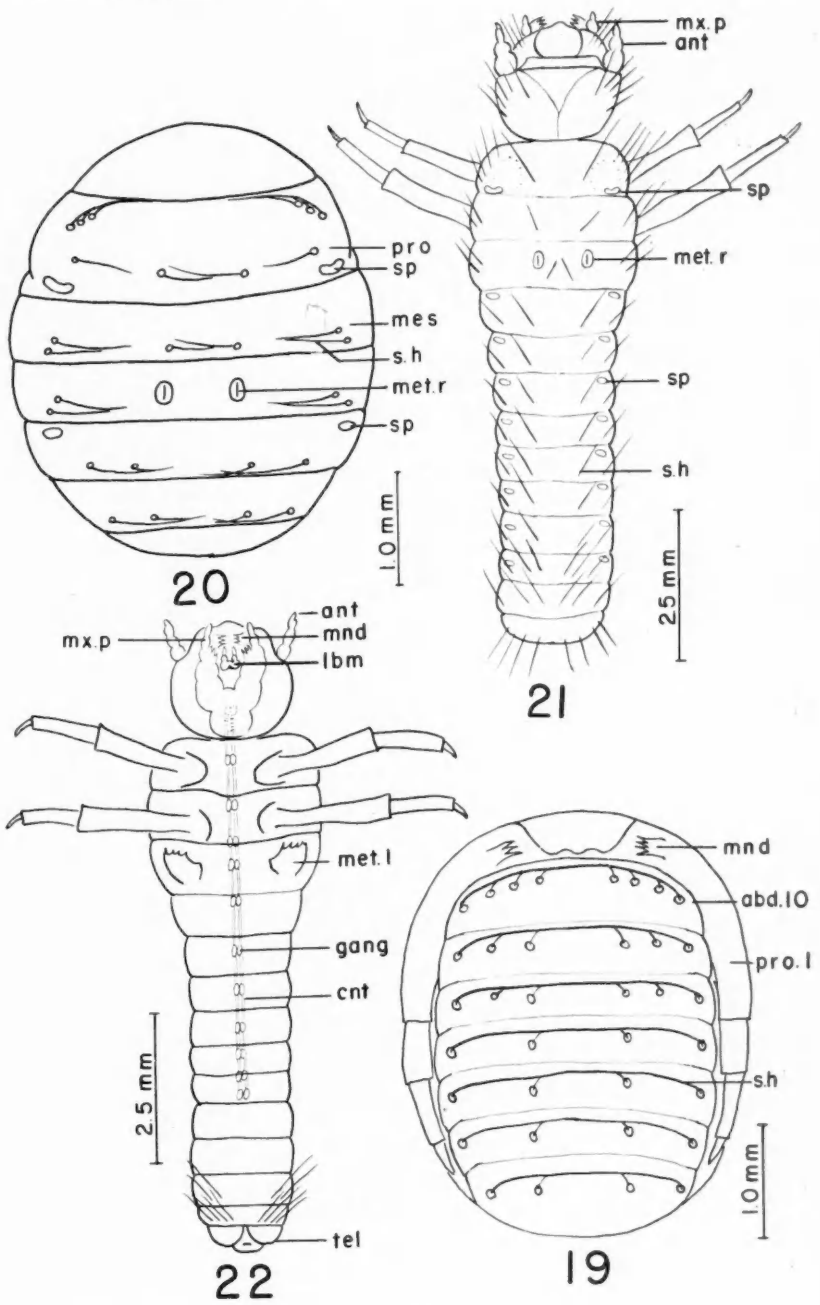
EXPLANATION OF PLATE IV

FIG. 19. Embryo in the fifteenth day, just prior to hatching; original ventral aspect. FIG. 20. Embryo in the fifteenth day; viewed from the original dorsal aspect of the egg. FIG. 21. Newly hatched first instar larva; dorsal view. FIG. 22. Newly hatched first instar larva; ventral view.

ABBREVIATIONS: *abd 10*—tenth abdominal segment; *ant*—antenna; *cnt*—intersegmental connective; *gang*—ganglion; *lbm*—labium; *mes*—mesothorax; *met. l*—specialized metathoracic leg; *met. r*—dorsal metathoracic ridge; *mnd*—mandible; *mx. p*—maxillary palp; *pro*—prothorax; *pro. l*—prothoracic leg; *s. h*—setal hair; *sp*—spiracle.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19

thoracic, and eight abdominal ganglia (Figs. 15 and 17). With the continued ventral curvature, the ganglia become pressed very close together and it is quite difficult to distinguish clearly the last ones from each other. Later they become completely covered by the cephalad growth of the caudal end of the abdomen. During the thirteenth day an additional pair of darkly staining clumps, the trichogens (*tr II*), can be seen close to the lateral margins of the segments. By the fourteenth day (Fig. 18) the embryo has increased considerably in length and with the ventrocephalad growth of the abdomen, the anal segment and abdominal segments VI to X are located in such a manner that their dorsal surfaces are visible on what was originally the ventral aspect of the egg. Meanwhile, the head and tail regions have been coming closer together.

Days 15 and 16: In the fifteenth day, just prior to hatching, the tip of the abdomen is in close approximation to the head (Fig. 19), and the conspicuous setal hairs (*s. h*) have been formed. At first these setal hairs are whitish in color, but they soon turn a dark orange hue and can be clearly observed even through the intact chorion of the living embryo.

The number of the large setal hairs on most of the segments is fairly constant. On the prothorax (Fig. 20) there are ten to twelve, on the mesothorax six, and on the metathorax some specimens had four, some five, and still others had six. On the abdominal segments (Figs. 19, 20) the first to the seventh segments have four setal hairs, the eighth and ninth each have six, and the tenth has eight.

Approximately two days before hatching is to occur, a pair of small spiracle-like structures, with narrow elongate ridges, appears on the dorsal aspect of the metathorax a little lateral to the mid-line (Fig. 20, *met. r*). They first appear as a pair of small, round, shallow depressions in the integument. Then the narrow longitudinally directed median ridge appears in each and soon turns brownish in color. In a short time the originally depressed structure rises and becomes quite flush with the integument of the metathorax. It was observed that these spiracle-like structures remain throughout the first larval stadium. Some specimens of second instar larvae showed small remains of these structures, whereas specimens of third instar larvae and subsequent stages showed no traces of them.

By the end of the fifteenth day the embryo resembles in almost all respects a newly hatched larva (Figs. 21, 22). The ventral nerve ganglia are in such a position that the original metathoracic ganglion now lies between the mesothorax and metathorax. The first abdominal ganglion is located in the metathorax, and the other abdominal ganglia have migrated one somite anteriorly.

DISCUSSION

The embryonic period of development of *Popilius disjunctus* Illiger can be divided into eight major stages, using externally visible morphological criteria which can easily be recognized even in the unstained embryo. The eight different stages have been identified by naming the structure or condition which is the most apparent new feature of each period of development: (I) Pre-Germ-Band, (II) Germ-Band,

(III) Segmentation, (IV) Appendage Formation, (V) Spiracle Formation, (VI) Lateral Growth, (VII) Ventral Curvature, and (VIII) Setal Hair Formation.

The following outline correlates the age of the embryo with the phase of development and lists the structural criteria for determining each phase:

I. Pre-Germ-Band—days 1 to 4
   1. No evidence of germ-band formation visible
II. Germ-Band—days 5 and 6
   1. Ventral plate disc- or pear-shaped—day 5
   2. Ventral plate hour-glass-shaped—day 6
III. Segmentation—day 7
   1. Appearance of segments in germ-band
   2. Elongation of embryo from two-thirds to almost the whole length of the long axis of the egg
   3. Appearance of rudiments of labrum and antennae in the cephalic lobes
   4. Appearance of stomodaeal invagination
IV. Appendage Formation—day 8
   1. Appearance of paired appendage rudiments on each somite
   2. Bending of the caudal part of the embryo over the posterior pole of the egg
   3. Appearance of neural ridges and future nerve ganglia
   4. Beginning of merger of the labrum anlage
   5. Appearance of proctodaeum
V. Spiracle Formation—day 9
   A. Early
      1. Appearance of paired spiracles on mesothorax, metathorax, and first eight abdominal segments
      2. Completion of fusion of labrum anlage
      3. Beginning of lobed condition of the mouthparts
      4. Thoracic legs divided into two podites
      5. Telson appearing bilobed
      6. Covering of stomadaeum and proctodaeum
      7. Position of antennae lateral to the stomodaeum
   B. Late
      1. Thoracic appendages divided into three podites
      2. Disappearance of abdominal appendages, except the pleuropodia
      3. Shift of the mesothoracic spiracles to the prothorax
      4. Head lying over the anterior pole of the egg
      5. Tail lying entirely ventrally
VI. Lateral Growth—days 10 and 11
   1. Lateral growth and dorsal expansion of embryo
   2. Disappearance of the metathoracic spiracles
   3. Ventral nerve ganglia becoming bilobed; with intersegmental connectives
   4. Envelopment of yolk half completed by day 11, and nearly complete at the end of the eleventh day
VII. Ventral Curvature—days 12 to 14
   1. Ventrocephalad growth of the caudal end of the abdomen toward the head
   2. Completion of the dorsal closure
   3. Appearance of trichogens
      a. First pair per segment on day 12
      b. Second pair per segment on day 13
   4. Claws appearing on tips of pro- and mesothoracic legs
   5. Metathoracic legs appearing paw-like in form
VIII. Setal Hair Formation—days 15 and 16
   1. Appearance of large setal hairs, first white, then dark orange in color
   2. Head and tail in close approximation
   3. Appearance of small dorsal ridges on metathorax

Using the above outline as a guide, the collector can, upon removing the chorions of the eggs, easily ascertain both the approximate ages in days as well as the precise developmental phases of eggs of unknown ages. Because of the time and inconvenience involved in obtaining eggs from ovipositing female beetles in the laboratory, this method of determining the stages of development allows for collection of far greater numbers of eggs from the field for use in developmental studies. Furthermore, since there is considerable variation in the degree of development of eggs incubated in the laboratory for the same length of time, the method is a more accurate way of determining the stage of development than by expressing the number of days of incubation. Because the removal of the chorion is necessary, it is obvious that this method cannot be utilized in ascertaining the developmental stages of eggs to be studied in the living state.

The above outline of the correlation of age and degree of development of the embryo has fulfilled not only the first objective of the study, but also forms, in large measure, the basis for fulfillment of the second. The second objective was, namely, to establish topography and landmarks for further, more detailed embryological studies. With the aid of the outline and the illustrations, sections of passalus eggs can be oriented and more easily interpreted. Preliminary sections of embryonic stages have been confusing because of the unusual positions which the embryo assumes during various phases. With the external features of the embryonic stages determined, the detailed embryological studies of the species should be facilitated. The third objective was to compare certain phases of the embryology of the externally visible structures with conditions found in other members of the group.

Formation of the Germ-Band: Among the Coleoptera germ-band formation has been described as occurring as early as the thirty-fifth hour in *Brachyrhinus* by Johannsen and Butt (1941). In *Popilius disjunctus*, however, the first indication of germ-band formation was observed in eggs which had been incubated for five days. In these eggs the ventral plate was a small, darkly staining, disc-shaped area located on the ventral surface of the egg, approximately in the anterior third (Fig. 1).

The germ-band of passalus does not attain the length comparable to that of the germ-bands of some other insects, and it remains completely superficial to the yolk in all stages of development. In *Hydrophilus*, Korschelt and Heider (1899), while the germ-band grows in length, its posterior portion bends around the posterior pole of the egg and becomes immersed in the yolk. This occurs in other coleopterans as well. In *P. disjunctus*, however, only the phenomenon of the germ-band bending around the posterior pole of the egg was observed (Fig. 9). Blastokinesis and rotation, or reversal of the position of the embryo, are observed at this stage in many insects, but in passalus blastokinesis is delayed until a much later stage, namely, until the ninth and tenth days, during the processes of appendage and spiracle formation. Furthermore, in passalus there is no rotation of the embryo strictly comparable to such a process in other species.

Segmentation: Superficial examination of the embryo of *Popilius* in the stage of segmentation reveals no evidence of segmentation of the

surface areas. The layer below the surface, however, appears to be divided into definite somites, and this suggests that segmentation occurs initially in the mesoderm, a condition which is typical throughout the class, with the exception of *Pieris*. A study of sections of this stage is necessary before this fact can be verified.

The presence of ten abdominal segments plus a telson in the definitively segmented germ-band of passalus is typical of insects in general. As in *Brachyrhinus* and the lepidopteran *Pieris*, the three segments of the thorax are formed first, followed by those of the abdominal and cephalic regions (Fig. 5). This is in contrast to the situation in *Hydrophilus*, where the anterior and posterior parts of the germ-band develop more rapidly than the middle part. In the cephalic region of passalus a procephalic, an antennal, and three gnathal segments are clearly visible. The formation of the pit-shaped stomodaeal invagination occurs during the seventh day, in the stage of segmentation, as in *Brachyrhinus*, and precedes the formation of either the appendage rudiments or the proctodaeum, which is typical of most insects.

The labrum originates from paired, prominent elevations rostral to the stomodaeal invagination, prior to the appearance of the appendage anlage (Figs. 7, 8), and fusion of the two prominences in the midline is completed in the ninth day, during the stage of spiracle formation (Fig. 9). The manner of origin and the subsequent history of these labrum anlage, occurring similarly in *Hydrophilus* and others, lends support to the view held by some writers that the labrum represents a pair of fused, preoral appendages, homologous to the gnathal appendages.

Appendages: The antennae, which arise at the posterior margin of the cephalic lobes at approximately the same time that the other appendage rudiments appear (Fig. 8), migrate rostrally so that in the ninth day of incubation they are located lateral to the stomodaeal invagination. With further migration forward, they finally come to lie rostral to the mouth. Many investigators have described this rostral shift of the antennae, which is a common occurrence in insects.

The gnathal appendages, which are transformed into the mouthparts, appear as small protrusions during the eighth day of incubation (Fig. 8, *gn. ap*). Gradually enlarging, they become lobed during the ninth day (Fig. 10). During the tenth day (Fig. 13) the second maxillae approach each other mesially and unite to form the labium. Further, more detailed studies of the mouthparts during the embryonic history were not made nor intended at this time.

The thoracic appendages arise earlier, develop at a faster rate, and therefore appear larger than the other segmental appendages. The three pairs of thoracic legs parallel each other in development until the tenth day (Fig. 13), after which the first two pairs are seen to be considerably larger than the third. The metathoracic legs remain smaller than the others throughout the remainder of embryonic development, and become specialized into small, paw-like structures. During larval life the modified metathoracic legs and a roughened file-like plate, which develops on the coxa of the mesothoracic legs, serve as larval organs of stridulation, as is well known.

The abdominal appendages in passalus appear during the eighth day of development (Fig. 8, *abd. ap*), remain small and rudimentary, and then disappear at the end of the ninth day. The first abdominal appendages, however, do not follow the same course of development as those of the last nine. The first abdominal appendages, or pleuropodia, are larger and persist longer. They are somewhat leg-like in appearance and during the eleventh day they divide into two podites (Fig. 13, *plpd*). By the twelfth day the pleuropodia appear as small, pit-like depressions with a thin flap extending ventrally (Fig. 17), and just before hatching disappear completely. The present study sheds no light on their possible significance in this species, but in other insects the pleuropodia may have secretory or excretory functions.

Spiracles: The spiracles appear simultaneously in the mesothoracic, metathoracic, and first eight abdominal segments during the ninth day of development (Fig. 10) with the mesothoracic pair considerably larger than the others. In passalus the spiracles are definitely located within the segment, rather than in the transverse conjunctivae as has been described for some other species. The only changes in position and number of spiracles occur in the thorax. In the ninth day the first pair of spiracles, originally located in the mesothorax, have migrated to the posterior margin of the prothorax (Fig. 12). Still later in the ninth day the second pair of thoracic spiracles has migrated anteriorly and comes to lie between the mesothorax and metathorax. At ten days the second pair of spiracles disappears, so that the definitive number of spiracles has been attained, namely, one thoracic pair located on the prothorax, and eight abdominal pairs located on the first eight abdominal segments. When first clearly evident, the spiracles appear somewhat pit-like in form, located on little mound-shaped elevations. During stage VI, Ventral Curvature, they attain their definitive curved sausage shape (Fig. 17). The phenomena of migration and reduction in number of spiracles in *Popilius disjunctus* are typical of most of the insects.

Definitive Larval Body Form: During the ninth day the first extensive increase in width of the embryo begins, and the lateral expansion continues through the eleventh day when almost half of the yolk on the dorsal aspect is enveloped by the growing embryo.

Concomitant with the process of lateral growth and dorsal extension, there is a ventral curvature of the caudal end of the embryo followed by continued cephalad growth. The effect of this growth is the doubling back of the caudal end of the embryo in such a manner that the ventral surface of the posterior portion of the abdomen is applied to the ventral surface of the anterior portion. In the stage immediately prior to hatching the ventral curvature is completed, so that the anal segment and head of the embryo come into contact, both occupying the original anterior pole of the egg, with the dorsal surfaces of head, thorax, and abdomen lying next to the chorion.

With the complete enclosure of the yolk the embryo thus becomes a tubular structure containing remnants of the yolk inside. The completion of the dorsal body wall, or dorsal closure of the embryo, takes place in the seventh stage, about the twelfth day of incubation. At the time of the dorsal closure a pair of large, darkly staining cells, or

trichogens, can be seen on the dorsal surface of each thoracic and abdominal segment (Fig. 16). Later in the twelfth day two more of these trichogens can be seen on each segment at the lateral margins (Fig. 17). The trichogens, which are quite conspicuous as whitish bodies even in the unstained embryo, are ectodermal in origin, according to Johannsen and Butt, and are believed to be the setal mother cells which give rise to the large setal hairs of the embryo. In passalus the setal hairs arise very late in development, first appearing whitish in color. Just before hatching, the setal hairs become dark orange in color. The segmental arrangement of these fully developed hairs gives the embryo a striped, or banded appearance which is visible even through the intact chorion of the living egg and is a positive indication that hatching will occur within the next twenty-four hours.

Nervous System: In the fourth stage of development (Fig. 8) two longitudinal thickenings near the ventral midline of the embryo mark the first clear evidence of the formation of the central nervous system. Swellings occur along these thickenings in what appears to be segmental fashion. The swellings are the forerunners of the ventral ganglia, and there are indications of four cephalic, three thoracic, and ten abdominal ganglia. In the ninth day, stage V, only three of the cephalic ganglia are visible (Fig. 10), and at the end of the ninth day (Fig. 12) only two cephalic ganglia are visible. During the tenth and eleventh days, the sixth stage of development, there are one cephalic, three thoracic, and nine abdominal ganglia visible (Fig. 13). The last two abdominal ganglia have coalesced, and probably some of the cephalic ganglia have entered into the formation of the brain. However, the details of this phenomenon cannot be definitely established until sections or cleared and mounted specimens of the embryo are studied.

By the twelfth day, or seventh stage of development, the last three abdominal ganglia have merged, so that the definitive larval number of the ventral ganglia has been attained. By the time of hatching each of the eight abdominal ganglia has migrated one somite anteriorly (Fig. 22). Thus, in the larva there are one cephalic, four thoracic, and seven abdominal ganglia visible in the ventral midline. The curvature of the head and the cephalad growth of the abdomen make the determination of the segmental positions of the ganglia almost impossible from external observation, particularly between the twelfth and fifteenth days. The details of this phase of the development of the nervous system must likewise await microscopic studies of serial sections of the embryo. In general, the observations on the later stages of the embryonic nervous system agree with the conclusions reached by Cody and Gray (1938), however, those workers observed only three embryonic stages, of undescribed ages or definite stages of development.

Dorsal Metathoracic Ridges: The small, spiracle-like dorsal ridges on the metathorax are first evident approximately two days before hatching is to occur. As previously mentioned, they persist throughout the first larval instar. A few specimens of second instar larvae showed traces of these structures, but by the time the third instar has been attained they have disappeared without a trace. Preliminary studies of cleared larvae indicate that these structures are not connected with

any visible internal organ, rather they appear to be confined to the integument.

Gray (personal communication) is convinced that these structures are vestigial spiracles. However, it is quite obvious that these ridges are not the original metathoracic spiracles which have migrated dorsolaterally, since by the tenth day the second pair of thoracic spiracles has diminished in size and in a short time completely disappears. No traces of the ridges could be found from stage VI, Lateral Growth, through stage VII, Ventral Curvature. Early in stage VIII, with the formation of the setal hairs, the dorsal metathoracic ridges are first visible, and located in their definitive positions.

In view of the superficial spiracle-like appearance of these structures and the fact that they are located on the metathorax, one might concur with the idea that they are actually vestigial spiracles. However, their dorsal position, their origin only two days before hatching, their disappearance in the second larval instar, and the fact that the lateral metathoracic spiracles have already formed and disappeared by the tenth day of incubation, all tend to make this interpretation seem unlikely.

Only rarely in the Insecta do supernumerary thoracic spiracles occur. In *Japyx*, according to Imms (1934), there is a supernumerary pair of metathoracic spiracles, but these are located laterally. According to Comstock (1940), in the genus *Scutigera* and its allies among the Chilopoda, there are dorsal spiracles, but these are located singly in the midline of the segments that bear them. Vestigial spiracles, when observed, invariably occur on the segment in the same relative position as the normal functional openings.

There is no evidence that any ontogenetic significance should be attached to these structures in passalus, in contrast to the many examples of vestigial organs in other animals. If, however, vestigial structures are construed to be merely nonfunctional, then it is not inappropriate to refer to these dorsal metathoracic structures as vestigial and transitory in nature. Their homology to spiracles is not substantiated by the present study, and some other, as yet undetermined significance, if indeed there is one, must be attached to them.

SUMMARY

1. Because of the difficulties in securing adequate numbers of known aged eggs of *Popilius disjunctus* Illiger for embryological investigations, the major embryological phases of development were established by correlating the stages of development with embryos of known ages. The plentiful eggs of unknown ages can easily be collected from the field during the egg-laying season, and upon removal of the chorions, can be placed in their proper developmental sequences. The following eight readily recognizable stages were identified, correlated with the age of the embryo incubated at 28° C:

I. Pre-Germ-Band—days 1 to 4
II. Germ-Band—days 5 and 6
III. Segmentation—day 7
IV. Appendage Formation—day 8
V. Spiracle Formation—day 9

VI. Lateral Growth—days 10 and 11
VII. Ventral Curvature—days 12 to 14
VIII. Setal Hair Formation—days 15 and 16

2. Germ-band formation occurs during the fifth day of incubation. The ventral plate appears as a disc-shaped area in the anterior third of the ventral side of the egg. The plate soon becomes pear-shaped, then hour-glass-shaped. The germ-band itself assumes a more elongate outline.

3. Segmentation occurs during the seventh day, the thoracic region segmenting prior to the abdominal and cephalic regions.

4. Appendage rudiments are formed in the eighth day, and the caudal end of the embryo bends around the posterior pole of the egg. The abdominal appendages disappear before hatching, and the metathoracic appendages become specialized into paw-like stridulatory structures.

5. Spiracles are formed on the mesothorax, metathorax, and first eight abdominal segments in the ninth day. The first pair of thoracic spiracles migrates to the prothorax and the second pair disappears before hatching.

6. The nervous system at first includes four cephalic, three thoracic, and ten abdominal ganglia segmentally arranged. Fusions and migrations of ganglia occur during development, so that at hatching there are one cephalic, four thoracic, and seven abdominal ganglia visible in the ventral midline.

7. Blastokinesis occurs during the ninth and tenth days, with the head being located at the anterior pole of the egg and the tail having shifted well forward of the posterior pole. In the twelfth day the caudal end of the embryo begins its ventral curvature and cephalad growth.

8. Prior to hatching the head and tail are in close approximation near the anterior pole of the egg, with the dorsal surfaces of the sixth to tenth abdominal segments visible on what was originally the ventral aspect of the egg. Conspicuous, dark orange setal hairs on most of the body segments are indicative that hatching will occur within twenty-four hours.

9. A pair of spiracle-like ridges appears on the dorsal aspect of the metathorax approximately two days before hatching is to occur. These structures persist throughout the first larval instar, but usually have disappeared in the second instar. They are probably vestigial in nature, but it is unlikely that they are homologous to spiracles.

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THE ORIGIN AND HISTORY OF THE BRITISH FAUNA, by B. P. BEIRNE. x+164 pp., 60 figs. (maps). Methuen and Co., Ltd. London. 1952. Price 18s.

Working with one of the world's best-known faunas and one which under present conditions exists in at least partial isolation, the author has attempted to trace its development, through the periods of advance and recession of the Pleistocene ice caps, to the present day. His methods of reconstructing the histories are based primarily on evidence provided by the present bionomics, taxonomy, and distribution of the animals, and by past environmental changes; though indirect, this is more important than the fragmentary evidence provided by paleontology and history. Examples are drawn chiefly from the land vertebrates and the Lepidoptera. The author reaches the conclusion that all surviving species of animals, or their ancestors, reached the British Isles from abroad, particularly from the European mainland; that the majority of these were post-glacial invaders, followed in importance by survivers from the Interglacial Periods, particularly the first, and from Glacial Phases, particularly the second. The periods of union and subsequent separation of England from the continent on the one hand and Ireland on the other have, of course, had an influence on animal distribution and development of faunas.

The book makes good reading and is thought provoking. Though not free from controversial aspects, as the author freely admits, it should help toward an understanding of the fauna with which it deals. It is a worthy chapter in the field of dynamic faunistics.—M. T. J.

NOTES ON THE PHLEBOTOMUS OF PANAMA (Diptera, Psychodidae)[1]

X. *P. aragaoi, P. barrettoi* AND TWO NEW SPECIES

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The species here considered are quite similar in both sexes, being separated by relatively small differences in the genitalia and the spermathecae. We have had considerable difficulty in associating the sexes, our conclusions being at variance with those of Floch and Abonnenc (1943) in certain cases. The matter can only be settled by careful rearings, but we believe our associations are at least more probable. The numbers of pleural setae and shape of the anterior abdominal sternites have proved useful in associating the sexes of these species.

In studying this small group, we are again impressed with the lack of correlation between the secondary sexual characters of the two sexes. Thus the styles of *aragaoi* C. L., *barretto* Mang. and *runoides* n. sp. are exceedingly similar, while that of *carpenteri* n. sp. is quite different. The spermathecae of *aragaoi*, *barrettoi* and *carpenteri* are very similar, but those of *runoides* are entirely different. It seems quite impossible as yet to predict the structures of one sex from a knowledge of those of the other sex. These four species share certain characters, such as the long ascoids with short proximal prolongations, the large eyes and broad heads, similar palpi, four-spined styles and absence of basal setae on the coxites or modifications of the parameres and the very similar cibaria. Aside from the four species from Panama, the following species appear to be closely related and are included in the subjoined keys on the basis of their published descriptions: *P. heckenrothi* Floch and Abonnenc, *P. inflatus* Floch and Abonnenc and *P. texamus* Dampf. A number of other species may belong here, such as *P. lutzianus* C. L., *P. brasiliensis* C. L., *P. coutinhoi* Mang. and *P. pascalei* Cout. & Barr., but we prefer not to include them until adequate material of both sexes is available to us.

KEY TO MALES

1. Tips of genital filaments simple 2
   Tips of genital filaments modified, hooked, twisted or inflated 3
2. Median spine of style on a well-marked tubercle, inserted closer to the basal paired spines than to the terminal spine ..... **barretoi**
   Median spine not on a tubercle, inserted half-way between basal spines and terminal spine ..... **texanus**
3. Tips of genital filaments expanded. Ascoids paired on all but last two antennal segments 4
   Tips of genital filaments hooked or twisted. Ascoids paired on all but last three antennal segments 5

[1]Costs of publication are paid by the Gorgas Memorial Laboratory.

4. Tips of genital filaments in shape of a spear head, lanceolate. Basal spines of style not paired, the dorsal one close to the median spine. Fifth palpal segment shorter than third and fourth together..... **runoides**
   Tips of genital filaments inflated before the apex, the latter drawn out into a long hook. Basal spines of style paired, at the same level. Fifth palpal segment longer than third and fourth together..... **inflatus**
5. Tips of genital filaments twisted like a cork-screw or a pig's tail. Parameres broad and flattened. Aedeagus very heavy and stout, bluntly and abruptly tapered at apex. Spines of style of a basal pair at nearly same level, a median dorsal spine on a short tubercle, and a terminal spine, ... **aragoai**
   Tips of genital filaments hooked like a button-hook. Parameres slender, more or less clubbed, curved upwards. Aedeagus very long and slender. Spines of style of a single basal, a median dorsal on a short tubercle, a subterminal and a terminal, the last two nearly paired so that the end of the style is unevenly Y-shaped..... **carpenteri**

KEY TO FEMALES

1. Spermathecae tubular, the spermathecae not sharply differentiated from their ducts, the former twisted like a cork-screw for a part of its length... 2
   Spermathecae globular or pear shaped, large and sharply differentiated from their ducts..... 3
2. Terminal annulate or wrinkled portion of spermathecae about four times as long as wide, not twisted. Twisted portion of two and a half or three complete turns. Ducts joined to form a short common duct..... **runoides**
   Terminal annulate or wrinkled portion of spermathecae about twice as long as wide. Twisted portion irregular and apparently of greater extent. Ducts opening separately into vagina. (*P. aragaoi* of Floch and Abonnenc), ... **inflatus?**
3. Ducts of spermathecae with wart-like or pustulate excrescences on proximal half, the ducts about eight times as long as greatest transverse diameter of spermathecae. Delta of wing venation short, one-fifth or less of alpha ..... **heckenrothi**
   Ducts of spermathecae smooth or annulate, not pustulate, less than three times as long as greatest transverse diameter of spermathecae..... 4
4. Ducts of spermathecae finely annulate. Spermathecae gourd-shaped or pear-shaped, the terminal knob a flattened raised plaque. Genital fork with small lateral expansions near apex of stem. Delta about half alpha; beta plus gamma about two-thirds alpha..... **carpenteri**
   Ducts of spermathecae smooth. Spermathecae spherical or oval. Stem of genital fork without lateral expansions..... 5
5. Terminal knob of spermatheca small and discrete. Ducts about 2.5 times greatest transverse diameter of spermathecae..... **texanus**
   Terminal knob of spermatheca a large plaque or diffuse patch of hairs..... 6
6. Spermathecae nearly spherical, the terminal knob a diffuse patch of hairs. Ducts about 2.6 or more times greatest transverse diameter of spermathecae, very thin-walled and tenuous. Stem of genital fork slender and cylindrical. Delta less than one-half alpha..... **aragaoi**
   Spermathecae oval, the terminal knob a raised, discrete, pigmented plaque. Ducts about three times greatest transverse diameter of spermathecae, relatively thick-walled. Stem of genital fork broad and flattened, its tip shallowly bifid. Delta over one-half alpha, the latter very long, at least twice beta plus gamma. Head unusually wide and flattened at vertex, nearly twice as wide as high..... **barrettoi**

In dealing with females of the three species *aragaoi*, *barrettoi* and *carpenteri*, whose spermathecae and cibaria are so similar, we believe certain minor characters may be of use in separating them, especially when, as is often the case, the spermathecae are much shrunken. We give below a key based on external characters, and including *P. runoides* for the sake of completeness.

1. Wing with alpha and delta very long, the latter considerably more than half the former. Five to seven lower mesanepisternal setae. Vertex of head flattened ..... **barrettoi**
   Wing with alpha and delta shorter, delta less than half length of alpha. Four or less, usually one to three lower mesanepisternal setae 2
2. Antennae with paired ascoids on all but the last two segments in both sexes. Setae on dorsal aspect of ninth tergite narrowly ligulate ..... **runoides**
   Antennae otherwise. Setae on ninth tergite simple, slender 3
3. Antennae with paired ascoids on all but the last three segments. Delta more than one-third alpha ..... **carpenteri**
   Antennae with paired ascoids on all segments, or with but a single ascoid on the terminal segment. Delta shorter, one-third alpha or less ..... **aragaoi**

Phlebotomus aragaoi Costa Lima

Plate I, figs. 1–8; Plate IV, fig. 23

1932, Mem. Inst. Osw. Cruz, 26 (1): 48, figs. 34, 60, 128–130 (♂; Minas Gerais, Brazil, from armadillo burrows). Barretto, 1947, Arq. Zool. Est. S. Paulo, 5 (4): 185–186 (full references). Floch and Abonnenc, 1943, Inst. Pasteur Guyane Francaise, pub. no. 61, pp. 11–14, figs. 6–7 (♂, ♀; Montabo, Fr. Guiana, from burrow of Paca); 1947, Bol. Ent. Venezolana, 6 (1): 18–19 (♂, in key). Barretto, 1950, An. Fac. Med. Univ. S. Paulo, 25: 109, 116 (♂, ♀; in key). Damasceno, Arouck and Causey, 1949, Rev. Serv. Esp. Saude Pub., Brasil, 1949: 819.

Male.—Wing length 2.03 to 2.12 mm. (Panama specimens), 1.89 to 2.03 mm. (Paraguay specimens). A rather large sandfly with moderately infuscated mesonotum, pleura and coxae. Abdominal hairs erect. Postspiracular setae 8–10, lower mesanepisternal setae 1 or none in Panama specimens, the Paraguayan material showing up to 14 post spiraculars and 1–3 lower mesanepisternals. Head height slightly less than length of proboscis and about three-fifths width of head. Basal antennal segments and palpi as in female, the end of third antennal segment reaching to or beyond end of fourth palpal segment. Newstead's scales scattered over distal third of second and all of third palpal segments. Ascoids as figured, paired on all but the terminal three segments of antennae. Cibarium with about eight small horizontal teeth and scattered small vertical teeth. Pharynx unarmed. Genitalia as figured, the filaments about twice as long as the pump, the plunger of the latter with small cup-like terminal expansion.

Female.—Wing length 2.178 to 2.27 mm. (Panama), 2.02 to 2.09 mm. (Paraguay); venation as figured. Similar to male in color and vestiture, showing 7–11 postspiraculars and 0–2 lower mesanepisternals in Panama material and 9–16 postspiraculars in those from Paraguay. Lateral aspect of eighth tergite with 0–2 setae, dorsal aspect of ninth tergite with fine simple setae. Proboscis about equalling head height; height of head about five-sevenths its width. Basal antennal segments and palpi as figured, third antennal segment reaching to level of end of third palpal segment when both attached to head. Ascoids as in male, paired on all segments but the last three, which are rather abruptly shorter than the next preceding segments. Cibarium as figured. Pharynx unarmed. Spermathecae as figured. Wings clothed with hairs and a few scales at base.

We have examined the following material of this species: 7 males and 7 females taken in a light trap at Mojinga swamp, near Ft. Sherman, Canal Zone, Sept. 1951 and Jan., Oct. and Dec. 1952, in light traps at

Gatun, C. Z., Sept. 1951 and Madden Dam, C. Z. Sept. 1951, F. S. Blanton coll.; 31 males and 4 females, Aca-Poi, San Pedro, Paraguay, the males from animal burrows, the females from animal burrows and a Shannon trap at light, various dates in April and May 1950, M. Hertig coll.; 8 males and 3 females from Brazil, the females numbered 838, all determined as ***aragaoi*** by Dr. O. Mangabeira but with no other data; 1 male, no. 810, Montabo, Fr. Guiana, "8–4–48," burrow, named and presented by Dr. H. Floch.

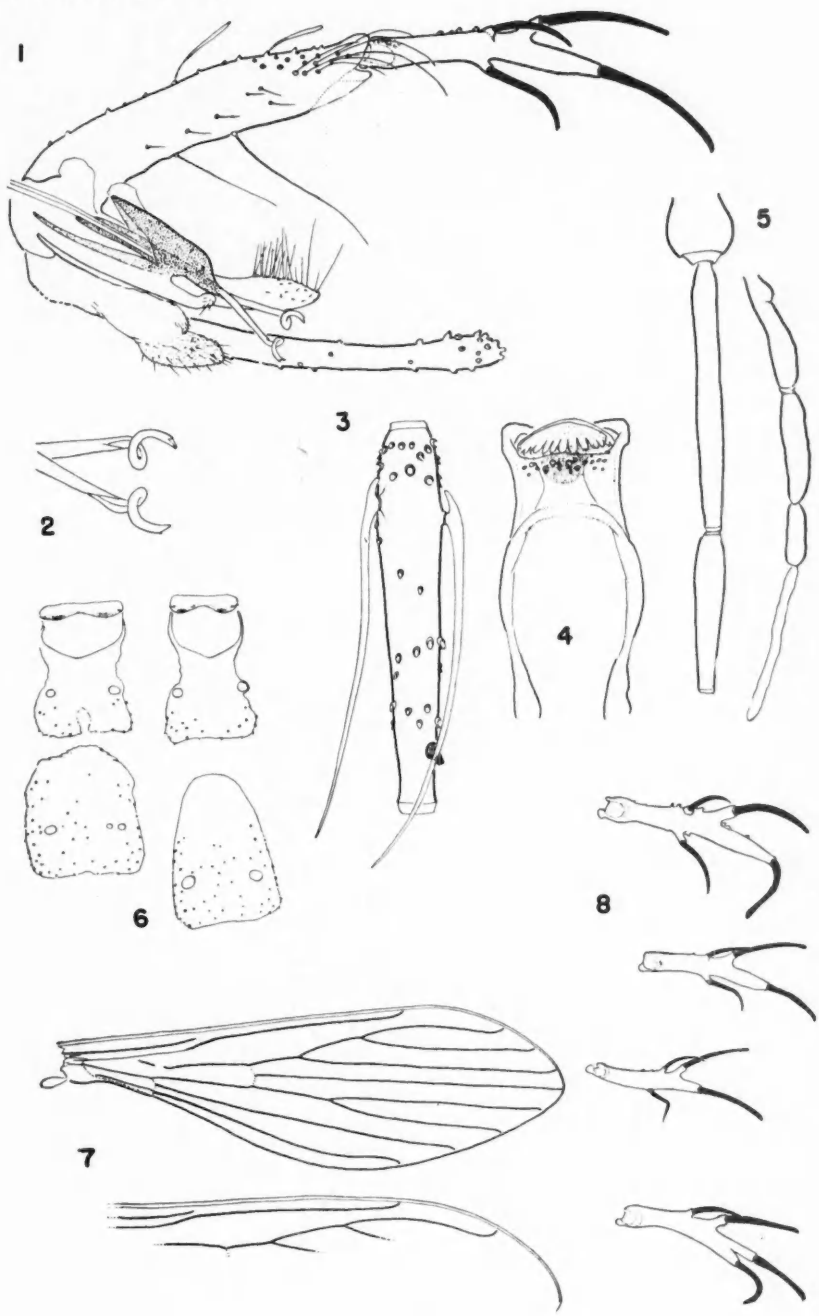
We associate the sexes on the basis of the following considerations. Both sexes have been taken together in Panama and in Paraguay and we have specimens from Brazil presumably taken together. Two of the other three similar Panama species, ***carpenteri*** and ***runoides***, have been taken in a number of other localities in the absence of ***aragaoi***, while the third species, ***barrettoi***, differs in both sexes in the longer delta and alpha of the wing venation, broader, flattened head and more numerous lower mesanepisternal setae. The non-sexual structural differences from ***carpenteri*** and ***runoides*** are slight, consisting in differences in the shape of the first two sternites and in shorter average delta of the wing venation.

The specimens thought by Floch and Abonnenc (1943, 1945) to be the females of ***aragaoi*** are very similar to those we believe to be the females of *P.* ***runoides*** n. sp., described herein. We think it very probable that these specimens are in reality the females of *P.* ***inflatus*** F. & A. 1944. The latter was described from males from burrows at Montabo, Fr. Guiana, the same locality which yielded the supposed females of ***aragaoi***.

P. ***heckenrothi*** Floch and Abonnenc (1942, Inst. Pasteur Guyane, pub. no. 38, pp. 8–10, fig. 4 and 1945, op. cit. pub. no. 100, p. 10–11, Pl. 4), described from 2 females from a burrow at Montabo, Fr. Guiana, is close to our specimens of ***aragaoi***, differing so far as we can tell only in having considerably longer ducts to the spermathecae, and in having scattered wart-like protuberances on the proximal half of the ducts. In our material, both from Paraguay and Panama, the proximal portion of the ducts is exceedingly thin-walled and tenuous, and the ducts open separately into the vagina, a fact not clear in the accompanying figure. In one specimen, both duct and spermatheca are filled with a granular substance, giving them a somewhat irregular or roughened appearance, not to be confused with the discrete warts or papules shown by Floch and Abonnenc in their second figure of ***heckenrothi*** (1945).

EXPLANATION OF PLATE I

Phlebotomus aragaoi. FIG. 1. Male genitalia, × 145. FIG. 2. Tips of genital filaments, × 293. FIG. 3. Segment IV of male antenna showing ascoids, × 350. FIG. 4. Female cibarium, × 350. FIG. 5. Female palpus and basal antennal segments, × 152. FIG. 6. First three abdominal sternites, female left, male right, × 89. FIG. 7. Wings, male above, female below, × 35. FIG. 8. Styles of, from top to bottom, ***barrettoi***, ***aragaoi***, ***runoides*** n. sp. and ***carpenteri*** n. sp., × 89.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Phlebotomus barrettoi Mangabeira

Plate II, figs. 9–13; Plate III, fig. 21; Plate IV, fig. 22

1942, Mem. Inst. Osw. Cruz, 37 (2): 148–152, figs. 58–62 (♂; Aura, Belem, Para, Brasil, in armadillo burrow). Barretto, 1947, Arq. Zool. Est. S. Paulo, 5 (4): 189 (full references). Floch and Abonnenc, 1945, Inst. Pasteur Guyane, pub. no. 106, pp. 6–7, fig. 4 (♂; Fr. Guiana). Damasceno, Arouck and Causey, 1949, Rev. Serv. Esp. Saude Pub., Brasil, 1949: 819. Rodriguez, 1950 [1952], Rev. Ecuatoriana Hig. Med. Trop., 7 (3–4): 25 (♂; Ecuador).

Male.—Wing length 2.31 to 2.36 mm.; venation as figured. A large sandfly with mesonotum, pleura and coxae moderately infuscated. Abdominal setae erect. Postspiracular setae 11–14, lower mesanepisternal setae 5–7, hair-like. Head height about one-third greater than length of proboscis and about three-fifths of head width. Basal antennal segments and palpi as in female, the end of third antennal segment reaching to about the end of the fourth palpal segment when both are attached to head. Newstead's scales scattered over distal half of second and all of third palpal segments. Ascoids as figured, paired on all but the terminal three segments of antennae, which are not abruptly shortened. Cibarium with a row of very fine, barely visible horizontal teeth and scattered minute vertical teeth. Pharynx unarmed. Genitalia as figured, the filaments about three times as long as the pump, simple.

Female.—Wing length 2.39 to 2.57 mm., venation as figured. A little larger than the male, but similar in color and vestiture. Lateral aspect of eighth tergite with from one to four setae; dorsal aspect of ninth tergite with slender setae. Proboscis about equalling head height from vertex to base of clypeus. Head about three-fifths as high as wide, the vertex markedly flattened. Basal antennal segments and palpi as figured, the end of third antennal segment reaching barely to middle of third palpal segment. Newstead's scales as in male. Ascoids as in male, paired on all segments but the last, where a single ascoid is present. Cibarium as figured. Pharynx unarmed, with weak wrinkles or ridges. Spermathecae as figured. Wings clothed with hairs, except for a few ligulate square-ended scales at base.

We have examined the following material of this species: 1 male, Brasil No. 1075, O. Mangabeira det; 2 males and 4 females, Mojinga swamp, near Ft. Sherman, Canal Zone, Nov. 1951 and Jan. and May 1952; and 1 female, Gatun, Canal Zone, 29 Aug. 1951; all the Canal Zone specimens taken in mosquito light traps by F. S. Blanton.

The males agree in detail with Mangabeira's description, with the specimen determined by him, and with Floch and Abonnenc's description. We associate the sexes on the basis of the very long alpha and delta of the wing venation, on the unusually numerous lower mesanepisternal setae and on the very characteristic and unusual flat head and

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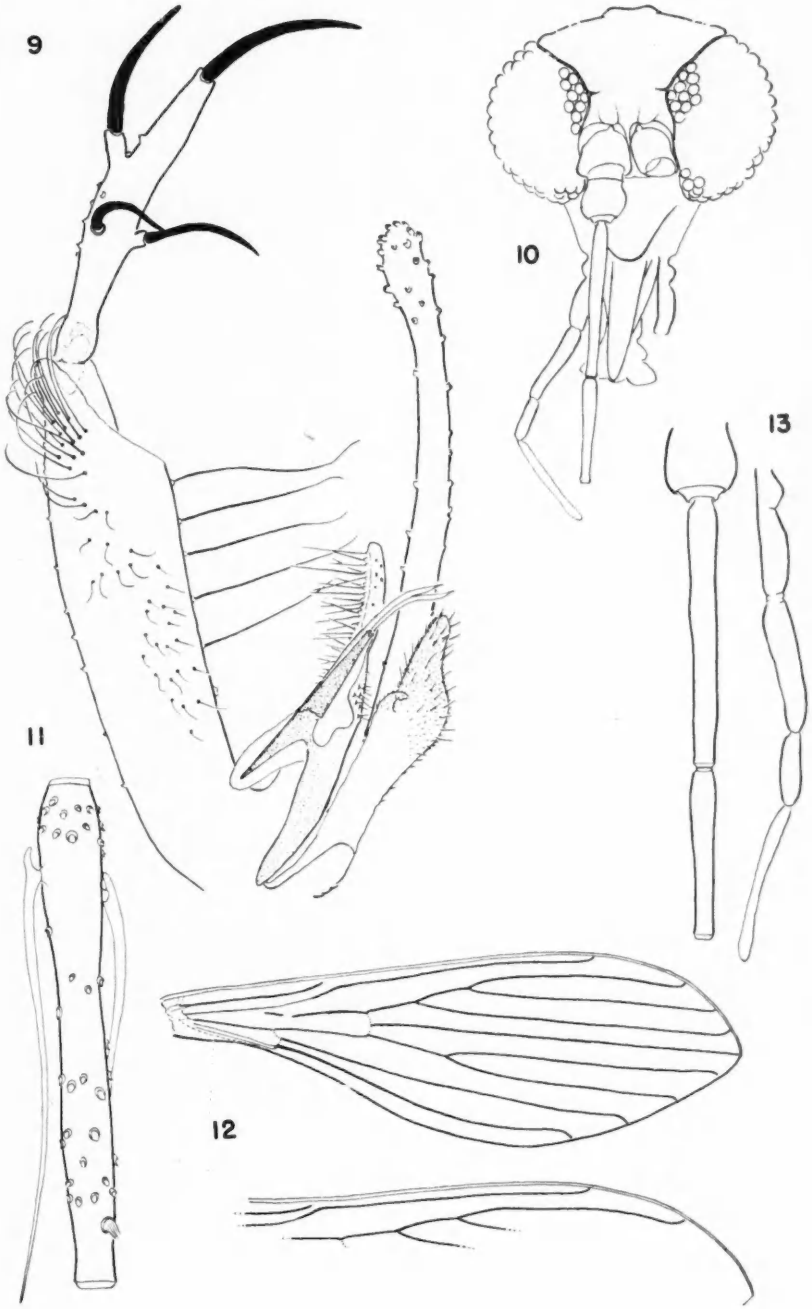
EXPLANATION OF PLATE II

Phlebotomus barrettoi. FIG. 9. Male genitalia, × 145. FIG. 10. Female head, frontal view, × 89. FIG. 11. Segment IV of male antenna showing ascoids, × 350. FIG. 12. Wings, male above, female below, × 35. FIG. 13. Palpus and basal antennal segments of female, × 152.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large eyes, a character noted in the original description and marked in both sexes. The large eyes and widened head seem characteristic of this group, but they are most marked in ***barrettoi***. The first and second abdominal sternites are about as in ***aragaoi*** and not sufficiently distinct to warrant figuring.

Phlebotomus carpenteri sp. nov.

Plate III, figs. 14–20; Plate IV, fig. 24

Male.—Wing length 2.09 to 2.27 mm.; venation as figured. A large sandfly with the mesonotum rather strongly infuscated, the pleura, coxae and abdomen more lightly brownish. Abdominal setae erect, hair like. Postspiracular setae 12–16, lower mesanepisternal setae 3–4. Head about one-third wider than height from base of clypeus to vertex and a little higher than length of proboscis. Palpi and basal antennal segments as figured; end of third antennal segment reaching about end of third palpal segment when both undetached. Newstead's scales cylindrical, but slightly enlarged apically, scattered over most of the length of the third and apical half of the second palpal segment. Ascoids long, as figured, paired on all but the terminal three segments, which are not abruptly shortened. Wing venation as figured. Cibarium with about eight small and slender horizontal teeth and numerous fine vertical teeth. Pharynx unarmed. Genitalia as figured, the filaments slightly more than twice as long as the pump, the latter with apex of plunger not greatly expanded, cup shaped. First and second sternites as figured.

Female.—Wing length 2.15 to 2.47 mm. Similar to male in color and vestiture. Lateral aspect of eighth tergite without setae, dorsal aspect of ninth tergite with only sparse hair-like setae, no scales. Cerci rather long. Proboscis a little less than head height, the head much wider than high. Basal antennal segments and palpi as in male, when attached to the head the third antennal reaches to about the end of third palpal. Newstead's scales as in male. Ascoids as in male, but paired on all segments, including the terminal one, or the terminal segment may have but one ascoid. Cibarium as figured. Pharynx unarmed. Spermathecae as figured. Wing venation as figured; wing clothed with setae except for striate, square-ended scales at base.

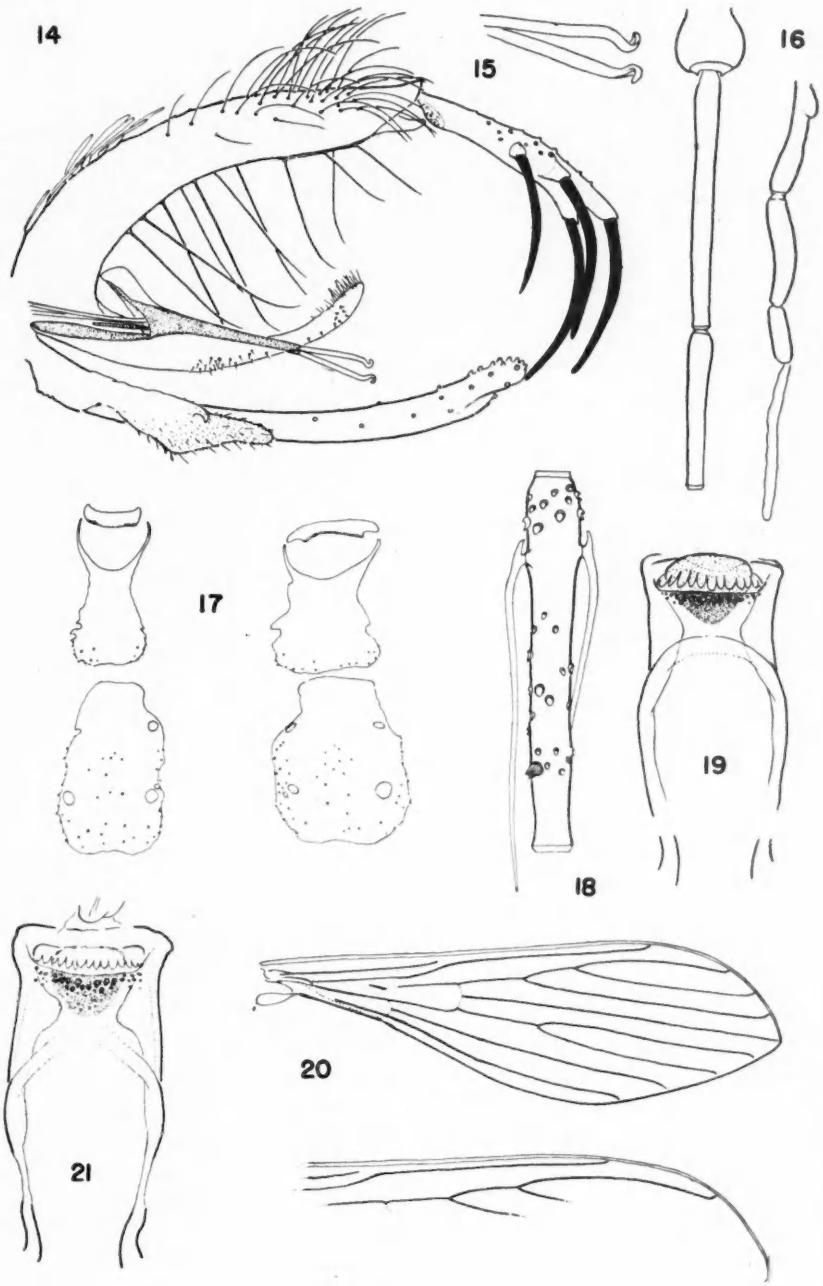
Holotype male, slide 1345, Chiva Chiva, Canal Zone, October 1948, in mosquito light trap. Col. S. J. Carpenter coll.

Allotype female, slide 2301, vicinity of Pacora, Panama Province, Panama, 13 August 1950, in animal burrow in forest. M. Hertig coll.

EXPLANATION OF PLATE III

Phlebotomus carpenteri n. sp. FIG. 14. Male genitalia, holotype, × 145. FIG. 15. Tips of genital filaments, same specimen, × 293. FIG. 16. Palpus and basal antennal segments of male, × 152. FIG. 17. First three sternites, male left, female right, × 89. FIG. 18. Segment IV of male antenna, showing ascoids, × 350. FIG. 19. Female cibarium, × 350. FIG. 20. Wings, male above, female below, × 35.

Phlebotomus barrettoi. FIG. 21. Female cibarium, × 350.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Paratypes, 16 males and 33 females mounted on slides from the following localities: Old Panama, 9 Aug. 1943, in holes in ruins (1 ♀); Rio Chico Hydrographic Sta., upper Rio Pequeni, Panama, 20 March 1948, in animal burrow (1 ♀); Chiva Chiva, Canal Zone, October 1948, light trap (2 ♂ 1 ♀); Paraiso, Canal Zone, Oct. 1948, light trap (1 ♀); Tocumen Airport, Panama, 22 Jan. 1949, light trap (1 ♂); Juan Mina, Canal Zone, Jan., Aug., Sept., Nov., Dec., 1949, Jan., Feb., Apr., Oct., Nov., 1950, in light traps (13 ♂, 25 ♀); vic. Pacora, Panama, 13 Aug. 1950, in animal burrows in forest (3 ♀); Mojinga swamp, nr. Ft. Sherman, Canal Zone, 5 Sept., 1951, in light trap (1 ♀).

In addition we have identified and stored unmounted or discarded over 300 specimens of both sexes from the above and about 20 additional localities in Panama and the Canal Zone. We have material from Darien (Patiño Point), Panama, Cocle (El Valle), Colon, Bocas del Toro (Almirante) and Los Santos (Las Tablas) Provinces, from both coasts of the isthmus in the Canal Zone, and from Costa Rica (Suerre, Guapiles). The species is most abundant along the Pacific coast at low elevations (no specimens from Cerro Campana or La Victoria in the hills, and but one from El Valle) and in the Canal Zone on both coasts. We have but a single specimen from Almirante, in the wet Atlantic coast rain forest, where much collecting has been done.

With the exception of a specimen from crevices in masonry and a few from animal burrows, all our material has come from fan-type mosquito light traps or Shannon traps with gasoline lanterns, so that we know nothing of the feeding preferences. The species has been taken in all months of the year and our records do not indicate any very marked seasonal variation in numbers.

Most of the light trap material was collected under the direction of Col. S. J. Carpenter, M.S.C., to whom the species is gratefully dedicated, and his successor Lt. Col. F. S. Blanton, who has contributed the bulk of material taken in the last year and a half.

Phlebotomus runoides sp. nov.

Plate IV, fig. 25; Plate V, figs. 26–33

Male.—Wing length 1.99 to 2.34 mm. A medium sized sandfly, the mesonotum, dorsum of abdomen and coxae moderately infuscated. Abdominal setae erect or semi-erect. Postspiracular setae 8–16, lower mesanepisternal setae 1–3. Head height nearly twice length of proboscis, the head very much wider than high, though vertex not flattened. Basal antennal segments as figured, the end of third antennal segment reaching to middle of fifth palpal segment when both are attached to

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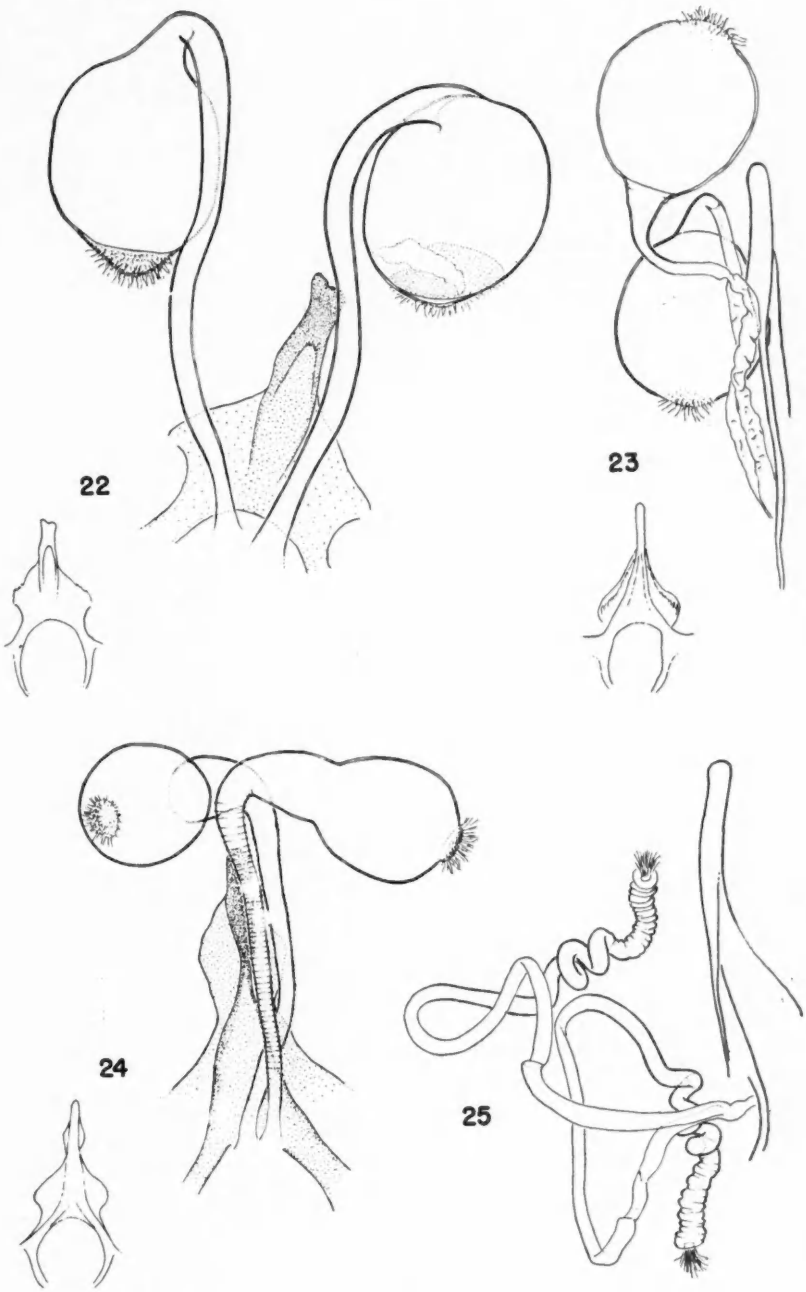
EXPLANATION OF PLATE IV

Phlebotomus barrettoi. FIG. 22. Spermathecae, × 293, and genital fork, × 145. Drawn after mounting in balsam from a Panama specimen.

Phlebotomus aragaoi. FIG. 23. Spermathecae, × 293, and genital fork, × 145. Drawn in phenol from a Paraguayan specimen.

Phlebotomus carpenteri n. sp. FIG. 24. Spermathecae, allotype, × 293, and genital fork, × 145. Drawn after mounting in balsam.

Phlebotomus runoides n. sp. FIG. 25. Spermathecae, allotype, × 293. Drawn in phenol after KOH.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the head in a mounted specimen. Newstead's scales rather long and slender, scattered over apical half of second and most of third palpal segments. Ascoids long, reaching or exceeding the ends of their respective segments and with a short proximal prolongation, present on all but the last two segments, which are shorter than those preceding. Wing venation as figured. Cibarium with about eight slender horizontal teeth and fairly numerous small vertical teeth; pharynx unarmed. Genitalia as figured, the filaments a little more than twice as long as the pump.

Female.—Wing length 2.01 to 2.26 mm. Similar to male in color and vestiture. Lateral aspect of eighth tergite with generally one or two setae, often with none. Ninth tergite with narrowly ligulate setae. Proboscis considerably less than head height, the head wider than high. Third antennal segment shorter, palpi considerably longer than in male, so that the end of the third antennal segment reaches only to middle of fourth palpal when both are attached to head. Ascoids as in male, absent from last two antennal segments, which are shorter than the one preceding. Cibarium as figured; pharynx unarmed. Spermathecae as figured. Wing as in male, clothed with hairs and a few ligulate square-ended scales at base.

Holotype male, slide 3593, Almirante, Bocas del Toro Province, Panama, 25–27 July, 1951. Taken between buttressed roots of forest trees. A. Quiñonez coll.

Allotype female, slide 772, La Victoria, Cerro Jefe, Panama Province, Panama, 2400 ft. elev., 23 Jan. 1947, in buttresses in forest.

Paratypes, 33 males and 24 females mounted on slides from the following localities: Barro Colorado Island, Canal Zone, 25 July 1944, taken in animal burrows by O. Mangabeira (7♂, 3♀); La Victoria, Cerro Jefe, near Pacora, Panama, 16 Dec. 1948, 1–2 Sept. 1950, in burrows, buttresses and at light (3♂, 2♀); Cerro Campana, Panama prov., Panama, 10 July 1949, in buttresses by L. E. Rozeboom (1♂); Juan Mina, Chagres river region, Canal Zone, 13, 22 and 27 Dec. 1949, in light trap by H. Trapido (3♂, 2♀); Mojinga swamp, near Ft. Sherman, Canal Zone, in mosquito light traps by F. S. Blanton, 15, 28 Aug. 1951 (5♂, 4♀), 4, 5 Sept. 1951 (12♂, 9♀), 27 Nov. 1951 (1♀), 18 Dec. 1951 (3♀), 31 Jan. 1952 (2♂); Almirante, Bocas del Toro Province, Panama, 27 Oct. 1951, in Shannon trap at light (1♀).

In addition to the above mounted specimens we have processed, identified and stored unmounted 42♂ and 35♀ from Mojinga swamp light traps, taken in Sept. (20), Oct. (14), Nov. (27), Dec. (13) and Jan. (3) and have identified but discarded 3♂ and 3♀ from the same locality taken in Dec. (1), Jan. (2) and Feb. (3). A single female from

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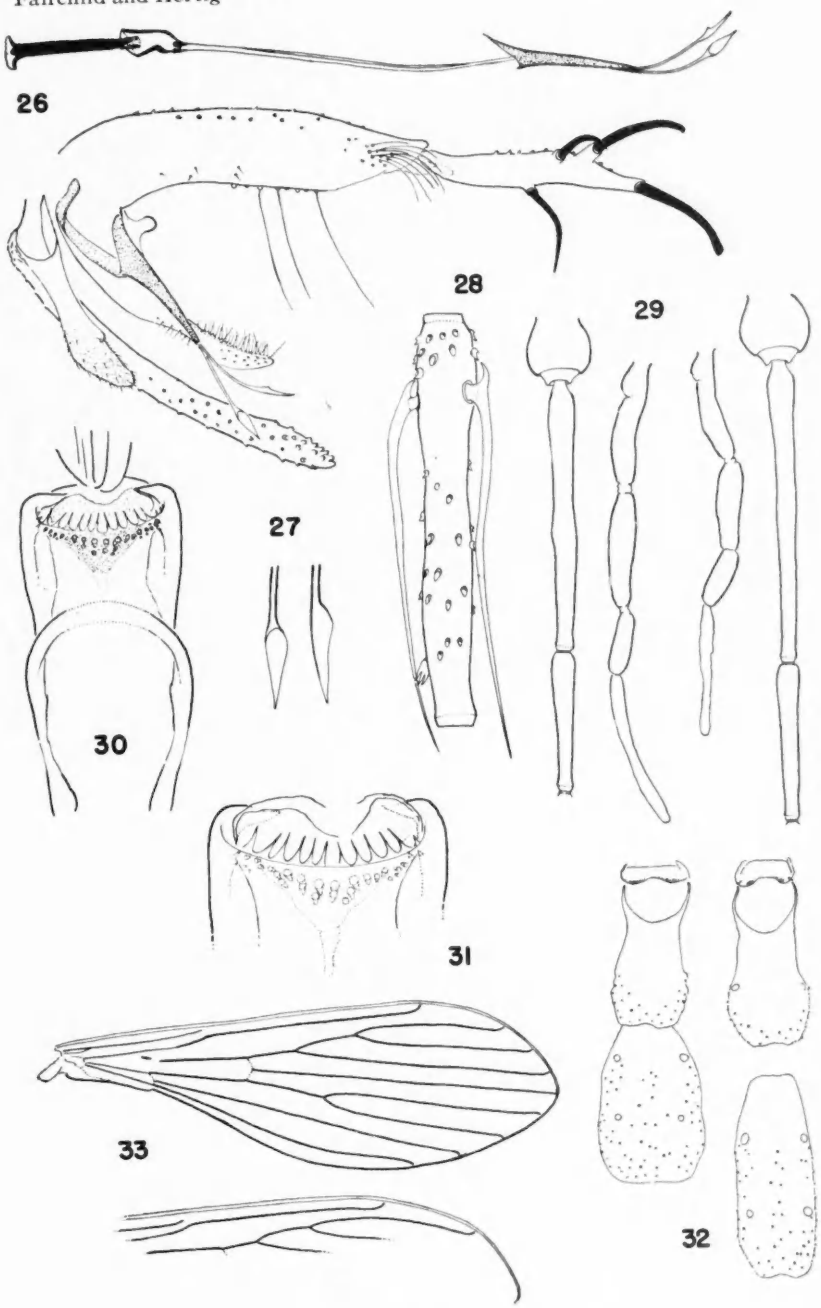
EXPLANATION OF PLATE V

Phlebotomus runoides n. sp. FIG. 26. Male genitalia and genital pump and filaments, holotype, both × 145. FIG. 27. Tips of genital filaments, × 292. FIG. 28. Segment IV of male antenna showing ascoids, × 350. FIG. 29. Basal antennal segments and palpi, male right, female left, both × 152. FIG. 30. Female cibarium, allotype, × 350. FIG. 31. Same, × 520. FIG. 32. First three sternites, female left, male right, × 89. FIG. 33. Wings, male above, female below, × 35.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Suerre, Guapiles, Costa Rica, 22 July 51, in armadillo burrow, R. Rosabal coll. has also been processed and stored.

The association of the sexes in this case is based on the similarity of structure, more especially of the first and second sternites, and the frequent appearance of both sexes in collections in the absence of other similar species. The females are closely similar to those believed by Floch and Abonnenc to be the females of *aragaoi* (1943, 1945). There are, however, certain differences. The spermathecal ducts of our species join close to the vagina and open to the outside through a common orifice, while Floch and Abonnenc's figure (1945) shows the ducts opening separately. The spermathecae themselves seem relatively longer, more defined and more clearly annulate in our species, and delta appears to be a little longer.

The male of *runoides* is separable from the males of the other species discussed here on the basis of the structure of the tips of the genital filaments, which are expanded into the shape of spear heads or javelin points, and on minor differences in the shape of the parameres and arrangement of the spines on the style. It seems closest to *P. inflatus* Floch and Abonnenc (1944), differing mainly in the lesser development of the same type of modification of the tips of the genital filaments. In *inflatus* the apices of the spear heads are attenuated into a long hooked filament, and the aedeagus is longer and more slender.

The association of the sexes in *carpenteri* and *runoides* has been rather difficult, as the external non-sexual characters are quite similar. The sternites in *runoides* are more elongate and slender and both sexes lack ascoids only on the last two segments of antennae. In *carpenteri* the sexes are dimorphic in respect to this character, the males lacking ascoids on the last three segments, while the females have ascoids on all segments, though there may be only a single ascoid on the terminal segment. *Carpenteri* has been taken in twenty-three localities, but in only four of these was *runoides* also found. The latter has been secured in three additional localities unaccompanied by *carpenteri*. It is of course, quite possible that we have reversed the sexes in this case, but only rearing tests will assure certainty.

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THE NEW ZEALAND ENTOMOLOGIST. The Entomological Society of New Zealand. A. D. Lowe, Secretary-Treasurer, Entomological Research Station, Ashburton.

Volume 1, number 2 of this publication, dated September, 1952, gives the following editorial statement: "It was decided that the Society should publish annually a journal containing notes which would not be suitable for publication in established journals in this country, yet which constitute news of entomological interest and value." The editor is B. B. Given, Nelson, New Zealand.—M. T. J.

SIMULIIDAE (DIPTERA) OF GUATEMALA. DESCRIPTIONS OF SIMULIUM (DYARELLA) ARDENI, N. SP. AND SIMULIUM (LANEA) JACOBSI, N. SP.[1]

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Federal Security Agency, Public Health Service, National Institutes of Health, National Microbiological Institute,[2]
Bethesda, Maryland,
and
Pan American Sanitary Bureau

The following two species of Simuliidae bring the total number known from Guatemala to forty-one. Descriptions of the larvae, pupae, and adults of all species, their biology, ecology, habits, and relationship to transmission of onchocerciasis in Guatemala will be presented in a future, more inclusive paper.

Simulium (Dyarella) ardeni, new species

While identifying blackflies collected in Guatemala by Dr. G. B. Fairchild during 1944, three interesting specimens were discovered that had been reared from pupae collected in a stream that harbored primarily *Simulium* (*Dyarella*) *mexicanum* Bellardi. More careful study showed these three flies to belong to a distinct species. Fortunately, amongst the three there were two males and a female, plus the cocoons and pupal cases, thus making possible the following description.

Male.—3.2 mm. long.

Head: Holoptic. Upper half of each eye light brown, with dark reddish-brown median patch; lower half dark reddish-brown. Antennae 730 μ long, 11-segmented, tapering; segment three equal to segments one and two taken together, shorter than four and five together, longer than segment 11; basal two segments and part of third yellow, the rest dark brown; all segments with grey pruinosity. Palpi light brown with grey pruinosity and several black hairs. Clypeus dark reddish-brown with grey pruinosity and long tan hairs. Occipital region black with grey pruinosity and black hairs.

Thorax: Mesonotum dark reddish-brown, with a very narrow black line extending from anterior margin to prescutellar region; on either side of median line there is a very broad band of white pruinosity, the area covered by the two together occupying about one-half the scutum; prescutellar region with long, black hairs; individual golden-yellow, scale-like hairs distributed over entire mesonotum, these being formed in groups of two or three as well as singly in prescutellar region. Humeral angles yellow with grey pruinosity and golden-yellow scale-like

[1]This paper is part of a study jointly directed by the Laboratory of Tropical Diseases of the National Microbiological Institute and the Pan American Sanitary Bureau, in cooperation with the Dirección General de Sanidad Pública of the Republic of Guatemala. The project was supported by a research grant from the National Institutes of Health, Bethesda, Maryland. Costs of publication are paid by the Pan American Sanitary Bureau.

[2]Laboratory of Tropical Diseases.

hairs. Pleura dark reddish-brown to black with grey pruinosity; prealar group formed by both yellow and black hairs; cluster of eight to ten short black hairs on mesepimeron; small group of black hairs on metepisternum, just posterior to spiracle. Scutellum light brown with grey pruinosity, long black hairs and several golden-yellow scale-like hairs. Postnotum black with grey pruinosity; no hairs. Stem of halter brown; the knob light tan. Wings, 3.1 mm. long and 1.2 mm. wide; Sc pilose on basal fourth; R_1 with spines and hairs along apical three-fifths, these beginning a short distance from point of branching of R_{2+3}; R_{2+3} simple, pilose along apical three-fifths; Cu_2 arcuate; discal cell absent.

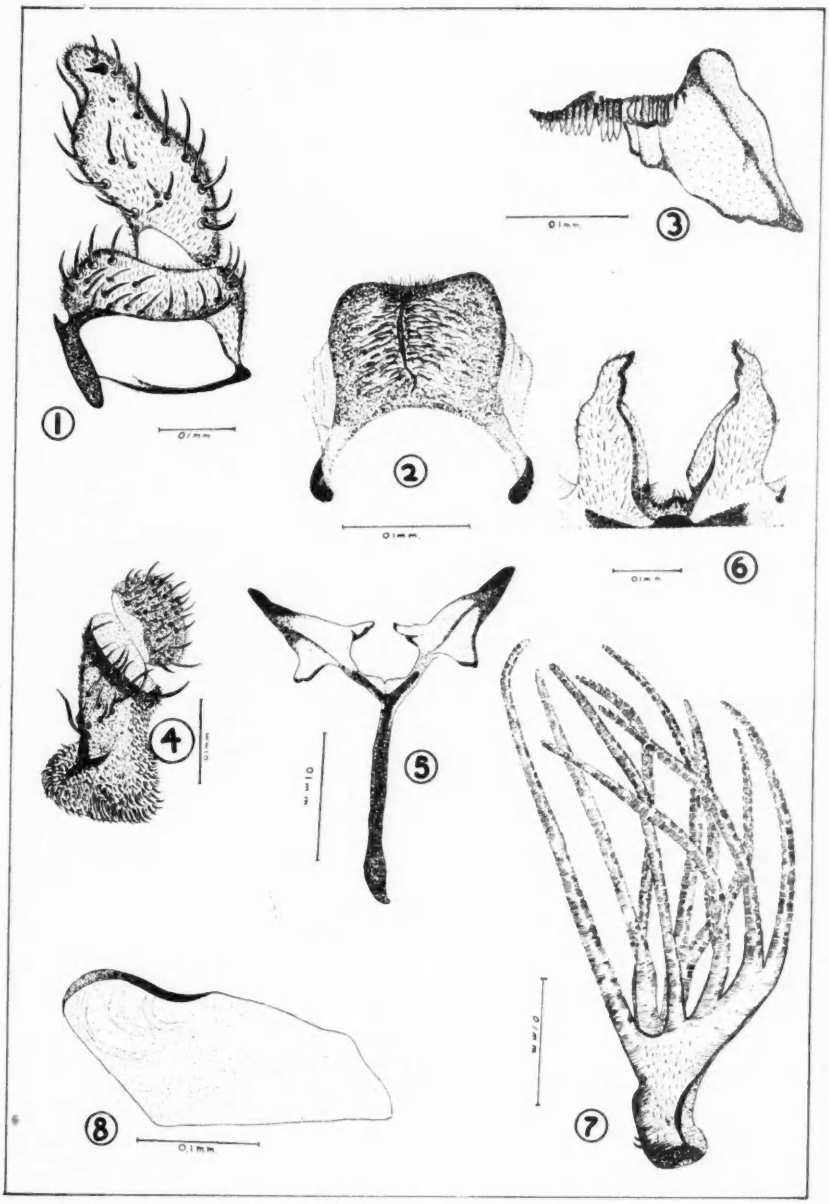
Legs: Leg 1—Length, 3.9 mm.; coxa, trochanter, and femur yellow; tibia black, its midregion somewhat lighter; tarsus black. Leg 2—Length, 3.6 mm.; coxa dark brown; trochanter yellow; femur yellow with black apical ring; tibia dark brown to black with somewhat lighter midregion, a small white ring at extreme base; basitarsus with basal two-thirds yellow, apical third black; segments two through five black. Leg 3—Length, 4.2 mm.; coxa dark brown to black; trochanter yellow; femur yellow with black apical ring; tibia brown with dark patches at base and apex, with very light tan ring at extreme base; basitarsus yellow with very small darkened area at extreme apex; segments two and three yellow, four and five black; calcipala well-developed and somewhat pointed, almost reaching pedisulcus; pedisulcus well-formed, deep, situated one-third distance from base of second tarsal segment.

Abdomen: Tergite and pleurites of segment one black, the tergite with light brown patch at its middle, its lateral regions with long brown hairs. Tergite of segment two dark brown to black, the anterior margin light brown. Other segments black, the pleural regions with grey pruinosity. All segments with short brown hairs. Sternites tan-pruinose.

Genitalia: Sidepiece (Fig. 1) somewhat rectangular in shape, approximately 1.3 times wider than long, the dorsal opening occupying about one-half its surface. Clasper (Fig. 1) 2.6 times longer than wide, 1.7 times the length of sidepiece; margins of clasper sinuous, well-marked opening on inner surface at base; apical region much narrower than rest of clasper, the apex itself rounded; terminal spine single, pointed, a distance from the apex. Both sidepiece and clasper with numerous long, stout, spine-like hairs. Body of adminiculum (Fig. 2) irregularly rectangular, much wider than long, the apical margin with marked concavity from which arise numerous hairs which are longer than any others on adminiculum; sides of adminiculum with small hyaline expansions; on ventral surface of body of adminiculum, passing longitudinally along midline, is a low keel which has numerous very short hairs on its ridge and somewhat longer hairs laterally; remainder of ventral surface with very few hairs, none on lateral expansions; basal prolongations with their ends well-sclerotized and spatulate. Adminicular arms (Fig. 3) with about 28 pointed teeth, parallel to one another and perpendicular to the long axis of the arm; lateral plate triangular, somewhat sclerotized, and wrinkled.

Female.—4.0 mm. long.

Head: Dichoptic. Eyes reddish-brown; height of fronto-ocular



Simulium (*Dyarella*) *ardeni*, n. sp. FIG. 1. Sidepiece and clasper of male (dorsal view). FIG. 2. Adminiculum of male (ventral view). FIG. 3. Adminicular arm and lateral plate. FIG. 4. Cercus and anal lobe of female. FIG. 5. Genital rod of female. FIG. 6. Ovipositors (flattened to show lateral face of each). FIG. 7. Pupal respiratory apparatus. FIG. 8. Cocoon (profile).

triangle 2.1 times the base. Antennae 750 μ in length, 11-segmented, slightly tapering; segment three shorter than either segments one and two taken together or segments four and five together, about equal to segment 11; first two segments yellow, the others brown. Palpi brown with black hairs. Clypeus coppery-red, with grey pruinosity and golden-yellow hairs. Frons dark reddish-brown to black with grey pruinosity and with short, fine, black hairs. Occipital region black, with numerous black hairs and a few white ones. Cornua of buccopharyngeal apparatus narrow, only slightly indented, with corrugated-like impressions; border of median space hyaline, smooth, without teeth.

Thorax: Mesonotum dark reddish-brown, completely grey-pruinose; small, fine, black hairs and very short, golden-yellow scale-like hairs distributed over entire mesonotum, the scale-like hairs never in groups and somewhat longer in prescutellar region; long, erect, black hairs on prescutellar region. Scutellum tan, with long, erect, black hairs, shorter recumbent black ones, and several golden-yellow scale-like hairs. Postnotum black with grey pruinosity, devoid of hairs. Pleura black with grey pruinosity. Stem of halter tan, the knob white and ovoid in shape; mesepimeron with cluster of yellow and black hairs; group of short white hairs on metepisternum, arising from yellow patch behind spiracle. Wings, 3.8 mm. long and 1.6 mm. wide; Sc pilose on basal fourth; R_1 pilose on apical three-fourths, also with spines on all but short basal portion of pilose area; R_{2+3} pilose except for short basal region; Cu_2 arcuate; discal cell absent.

Legs: Leg 1—Length, 4.4 mm.; coxa and trochanter yellow; femur yellow with dark apical patch; tibia yellow with apical fourth dark brown and with dark patch on outer surface of basal fourth; all tarsal segments dark brown. Leg 2—Length, 3.8 mm.; coxa dark brown; trochanter yellow; femur yellow with dark brown apical ring; tibia yellow with dark rings at base and apex, and with a dark longitudinal patch on its outer aspect which extends from the apical ring toward the base, reaching across three-fourths the length of the tibia; basitarsus with basal two-thirds yellow, apical third dark brown; segments two through five dark brown. Leg 3—Length, 4.6 mm.; coxa dark brown; trochanter yellow; femur yellow with dark brown apical ring; tibia and basitarsus as on leg 2; second tarsal segment with basal third yellow, apical two-thirds dark brown; segments three through five dark brown; calcipala well-developed, reaching pedisulcus; pedisulcus well-formed, deep, situated one-fourth the distance from base of second segment; heel of claw developed into pointed structure, no secondary claw.

Abdomen: Tergite of segment one tan with very light, long hairs on lateral areas; pleurites yellow. Segment two tan with posterior margin brown, completely covered with tan pruinosity. Segments three through five black with central brown patch and with posterior margins tan-pruinose; pleurites on each side of these segments yellow with one small brown patch; segments six through eight black with tan pruinosity. All segments with short black hairs. Sternites tan-pruinose, with short black hairs.

Genitalia: Cercus (Fig. 4) higher than long, posterior margin rounded, clothed with many heavy hairs and with several minute, spine-like ones. Anal lobe (Fig. 4) somewhat crescent-like, a large, mem-

branous, very hairy structure extending from it ventrally. Genital rod (Fig. 5) without basal dilatation, or at most, base very slightly expanded; arms of genital fork triangular in outline, the outer and apical angles heavily sclerotized. Ovipositor (Fig. 6) large, triangular in outline, 240 μ long, by 120 μ wide at base.

Pupa.—Dorsum of thorax and of first abdominal segment presenting lightly granular aspect. Dorsal surface of abdomen: Segment 1 with pale dentation along posterior margin which reaches segment 2; segment 2 with six simple spines; segments 3 and 4 each with eight simple spines. Ventral surface of abdomen: Segments 6 and 7 with four simple spines; segment 8 with four spines, the two inner ones simple, the outer ones bifid.

The respiratory apparatus (Fig. 7) of each side is composed of 10 filaments which are arranged, from above to below, in groups of 4–4–1–1 filaments; the filaments have a maximum thickness of 0.04 mm. and the entire apparatus reaches 1.2 mm. in length; filaments are smooth with superficial annulations.

Cocoon (Fig. 8): Length of base, 3.6 mm.; greatest length, 5 mm.; greatest width, 1.9 mm.; greatest height, 2.0 mm. Case with fine, parchment-like texture, dark orange-brown, with two to three ribbon-like markings near dorsal aperture which are woven into the cocoon itself; slipper-shaped, with distinct collar; rim around anterior aperture well-sclerotized, without ribbon-like festoons extending from it; lateral margins of cocoon not extended to form wings.

The male of *Simulium* (*D.*) *ardeni*, n. sp. appears closest to *S.* (*D.*) *yepocapense* Dalmat on the basis of the wide mesonotal bands of white pruinosity. However, it can easily be distinguished from the latter by the color of the hind femur, tibia, and basitarsus, and by the form of the clasper. In *ardeni* the femur is yellow with a black apical ring; the tibia is yellow with dark rings near base and apex; in *yepocapense* Dalmat both femur and tibia are black, except for a small yellow basal region on each. The basitarsus of *ardeni* is yellow with a very small darkened area at apex; that of *yepocapense* Dalmat has the basal half yellow, the apical half black. In *ardeni* the clasper is narrowed considerably near the apex and the terminal spine is at a distance from the apex, while in *yepocapense* Dalmat the clasper is broad at the apex, and the spine is almost terminal.

The female of *ardeni* most resembles *S.* (*D.*) *earlei* Vargas, Martínez, and Díaz insofar as they both have the mesonotum devoid of white-pruinose longitudinal bands and both have R_1 pilose on distal half to three-fifths only. However, the mesonotum of *earlei* Vargas, Martínez, and Díaz has the base color light brown, and is clothed with silvery-white scale-like hairs, these in groups of two and three near the anterior margin; the mesonotum of *ardeni* has the base color dark reddish-brown and is clothed with golden-yellow scale-like hairs, these never appearing in groups. The median space of the buccopharyngeal apparatus of *earlei* Vargas, Martínez, and Díaz has several wide, scale-like teeth, while that of *ardeni* is smooth, without teeth.

The pupa of *ardeni* is similar to those of *pulverulentum* Knab and *yepocapense* Dalmat, but can be distinguished by the characteristic ramification of the pupal filaments. The cocoon of *ardeni* is larger

than that of ***pulverulentum*** Knab, and the collar of the cocoon is much higher than that of ***yepocapense*** Dalmat.

Ecological Notes.—The pupae of ***Simulium*** (***Dyarella***) ***ardeni***, n. sp. were collected in the Department of Alta Verapaz, in a single stream, located on the northern slope of the Chuacús-Minas-Mico range which forms the most northern chain of mountains in Guatemala. The altitude of the region is about 4,600 feet. The river was about five to ten feet deep, with crystal-clear water and with little to no trailing vegetation; the current was swift, but with few rapids. The river passed through a narrow limestone gorge with banks five to 20 feet high. In general, ***Simulium*** spp. were scarce, the pupae of the specimens described being found on sticks and dead roots in a few existent rapids. The only other species found in the same stream was ***Simulium*** (***Dyarella***) ***mexicanum*** Bellardi.

Type.—***Holotype*** male (Accession Fair. 5–24A) reared from pupa collected in the Río Tzunutz, San Pedro Carcha, Alta Verapaz on November 16, 1944 by G. B. Fairchild; dissected adult, pupal exuvium and filaments mounted on seven slides, the cocoon preserved in alcohol. ***Allotype*** female (Accession Fair. 5–24B) reared from pupa collected with holotype; dissected adult and pupal exuvium mounted on six slides, the cocoon preserved in alcohol. ***Paratypes:*** Male (Accession Fair. 5–24C) reared from pupa collected with holotype; mounted on minuten nadel, the pupal exuvium and cocoon in alcohol. Four pupae and four pupal exuvia (Accession Fair. 5–24D); all preserved in alcohol.

The holotype and allotype have been deposited in the United States National Museum; the paratypes are in the collection of the author. This species has been named for Mr. Arden O. Lea, Jr., Assistant Entomologist with the Onchocerciasis Project in Guatemala.

Simulium (**Lanea**) **jacobsi,** new species

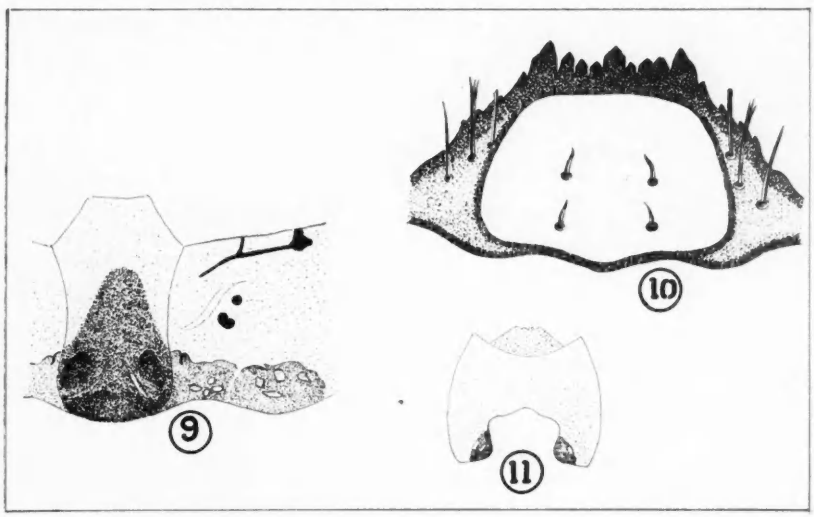
Amongst thousands of pupae and larvae collected in the Michatoya River, near Palín, Escuintla, a single larva was found that is completely distinct from all larvae of species known from Guatemala and Mexico, and from all other described species. A study of the well-formed histoblasts of the pupal respiratory apparatus permitted comparison with the pupae of species, the larvae of which have not yet been described. Further collections were made in the type locality, but these did not yield additional specimens of this species. Although it is considered preferable to have several specimens before describing the species as new, it is felt that the uniqueness of the larva under discussion and the desire to include all known forms in a forthcoming monograph of the blackflies of Guatemala, warrant the presentation of the description at this time. Attempts will be continued to secure more material.

Larva.—Total length, 4.6 mm. Head capsule 1.1 times longer than wide. Width of thorax 1.4 times the width of head. First four abdominal segments 1.3 times width of head; segments five through seven expanded laterally, about 1.4 times width of segments one through four; eighth segment sharply tapering.

Head: Light yellowish-brown. Frons-clypeus (Fig. 9) pale yellow with a very dark, irregularly-triangular design on its posterior half,

design not interrupted by non-pigmented regions, although clearly marked areas of contrasting intensity of color are visible; epicranial plates of either side with two large dark areas along posterior margin, each with three to four small markings within, those in the more lateral area appearing somewhat lighter than the surrounding region.

Each cephalic fan with 31–33 non-pectinate branches. Antenna 276 μ long, pale yellow, transparent, just reaching the apex of stalk of cephalic fan; four-segmented, the second segment divided into two near its midregion, giving the antenna the appearance of having five segments. Segments one and two about equal in length; either of these is longer than segment three. Segments one and two without transverse striations; segment one with longitudinal wrinkles.



Simulium (*Lanea*) *jacobsi*, n. sp. FIG. 9. Frons-clypeus and epicranial plate of larva. FIG. 10. Submentum of larva. FIG. 11. Ventral view of head capsule showing epicranial cleft.

Mandible with two flattened teeth on its inner margin, these being close together but not appearing to arise from the same base, the more distal one about twice the length of the other. Submentum (Fig. 10) with nine apical teeth, all of almost equal length, blunt, their lateral margins parallel; ventrolateral row composed of three fairly short stout hairs, the middle one trifid near its apex, the basal one simple; lateral margin of submentum with four tooth-like structures, the most apical one separated from the other three and appearing to emerge from the lateral margin of the outermost of the apical teeth; four small hairs emerging from ventral surface of median plate. Epicranial cleft (Fig. 11) dome-shaped, the apex with a slight concavity.

Thorax: Light cream color with purple collar near anterior margin. Post-clypeal sclerites in form of small, heavily-pigmented circles that are

well separated from each other. The pseudopod (thoracic proleg) has from 20–25 rows of hooks at its apex.

Abdomen: Light cream color with a transverse purple-colored band on posterior half of segments one through eight, these interrupted on segments five through seven by longitudinal white lines that cross through the transverse bands giving a striped appearance to that region of the abdomen; dark, comma-shaped structures present near the outer margins of the ventral surface of segments six and seven in the larvae of many Guatemalan species, absent. Anal gills in form of three very broad, conical structures that taper considerably from their base to apex; on the ventral surface of the middle trunk there is a single, short, finger-like projection emerging from near the mid-region; from near the same region of the right trunk, and extending to its apex, emerge two long projections; from the left trunk three such finger-like projections emerge and also extend to its apex; thus the anal gills have nine branches in all. Posterior sucker with 80–84 rows of hooks. The X-shaped sclerite is simple, well-sclerotized, with no pigmented patches between the arms. There are no rectal scales, ventral tubercles, or sclerotized plaques on the eighth segment.

This larva has been placed in the subgenus *Lanea* because it possesses the following characteristics: Mandible with two teeth on its inner margin; epicranial cleft well-formed and not reaching submentum; antennae four-segmented (rather than five-segmented, with further superficial divisions of second segment); posterior sucker with fewer than 150 rows of hooks; antennae lacking transverse striations; and rectal scales absent. *Simulium* (*L.*) *jacobsi*, n. sp. appears closest to *S.* (*L.*) *samboni* Jennings and *S.* (*L.*) *haematopotum* Malloch but can easily be distinguished from them by the completely dark patterns of the frons-clypeus, the non-pectinate condition of the branches of the cephalic fans, and the absence of ventral tubercles on the eighth segment of its abdomen.

Ecological Notes.—The stream in which this larva was found had a pH of 7.6, temperature of 26° C., a current speed of four and three-quarters feet per second, and a volume of 3130 gallons per second. The width of the stream was approximately 42 feet, its depth two feet. Its bed was composed of sand with numerous large and small stones, and with very little emergent or trailing vegetation. The altitude of the region was 4000 feet. The larva was collected from a twig floating on the surface of the water. The collection was made in June, during a lull in the rainy season.

Types.—***Holotype*** larva (Accession 12T-11) collected in the Río Michatoya, Finca El Llano, Palín, Escuintla on June 22, 1951, by J. Armando Castellanos and Jaime Rosales G.; dissected parts mounted on a single slide, deposited in the United States National Museum. This species was named for Dr. Leon Jacobs of the Laboratory of Tropical Diseases, Microbiological Institute, National Institutes of Health, U. S. Public Health Service.

GROWTH STUDIES WITH THE COCKROACH, PERIPLANETA AMERICANA (LINN.), FED VITAMIN-DEFICIENT DIETS SUBSTITUTED WITH CORRESPONDING ANTI-VITAMINS[2]

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The vitamin requirements of the German Cockroach were reported recently by Noland, *et al.* (1949). Their work showed that choline was the most critical vitamin, and that pantothenic acid and nicotinic acid were necessary to reach maturity. Pyridoxine, thiamine, and riboflavin were required by this cockroach for good growth and survival; while the lack of inositol, para-aminobenzoic acid, biotin, and vitamin K caused little or no decrease in their growth rate. It was interesting to note that in this study, the omission of folic acid sometimes seemed to cause growth stimulation. Noland, *et al.* (1949) concluded that there was a synthesis of riboflavin in the digestive tract of the German cockroach nymphs. Metcalf and Patton (1942), however, had found little or no bacterial synthesis of this vitamin in the cockroach, *P. americana*. Metcalf (1943) found very large amounts of most of the water-soluble vitamins stored in the malpighian tubes of the roach.

The vitamin requirements of some other insects have been studied, and Fraenkel and Blewett (1943) showed that several species of beetles required thiamine, riboflavin, nicotinic acid, biotin, pyridoxine, and pantothenic acid, and that choline was a growth factor. Inositol and para-aminobenzoic acid were possible growth factors. Fraenkel and Blewett (1947) found that folic acid was important for the growth of six other species of insects.

The discovery of competitive inhibition by analogues of metabolites has resulted in considerable attention being focused on the vitamin deficiencies which can be produced by the addition of these compounds to animal diets and bacterial cultures. An anti-vitamin has been defined by Wright (1947) as "any substance that interferes with the synthesis or metabolism of a vitamin." The functions of these analogues are characterized by inactivation or chemical destruction (thiamine by thiaminase) irreversible combination (avidin-biotin complex) or competitive inhibition. While instances of chemical destruction or specific binding of a vitamin has been observed, by far the commonest instance of anti-vitamin action is that of competitive interference or inhibition.

Several analogues of niacin have been reported to have anti-vitamin activity. Among these are alpha-picolinic acid, 3-acetyl pyridine, and pyridine-3-sulfonic acid. Woolley (1945) reported that niacin deficiency

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signs were observed in mice fed two or more mg. of 3-acetyl pyridine daily. This particular species was not susceptible to a niacin deficiency produced by the usual dietary means. Signs of the disease could be prevented by supplying sufficient amounts of nicotinamide. Gaebler and Beher (1941) fed 3-acetylpyridine to dogs and found an increased urinary excretion of N-methyl nicotinamide, but no deleterious effects. These same workers added pyridine-3-sulfonic acid to the diet of normal and niacin-depleted bitches and could show no effect on the health of the animals, excretion of N-methyl nicotinamide, or coenzyme content of the erythrocytes.

Snell and Shive (1945) reported both pantothenol and pantoyl-taurine produced growth inhibition in some microorganisms. This was specifically counteracted by pantothenic acid. The relationship was competitive over a wide range, and both were shown to be completely non-toxic for organisms which synthesize pantothenic acid. Their data often showed a resistance to one compound and a sensitivity to the other. Barnett and Robinson (1942) had previously reported a marked growth inhibition by pantoyl-taurine for *S. haemolyticus* and for some stains of *C. diptheriae* which was reversed by pantothenic acid.

Oleson, *et al.* (1948) showed that 4-aminopteroyl glutamic acid (aminopterin) was a powerful antagonist for folic acid and related metabolites. There appeared to be a competitive inhibition in rats and chickens, but the metabolite was quite toxic. Goldsmith, *et al.* (1950) studied the effect of folic acid analogues on the insect *Drosophila melanogaster*. They found that incorporating x-methyl folic acid, or 4-amino pteroylglutamic acid, in the basal ration resulted in a retarded rate of development and in many cases failure to complete the life cycle. This antagonistic effect could be annulled by addition of folic acid.

The anti-vitamin activity of the sulfa drugs for para-aminobenzoic acid has been known for some time. Another of the inhibitory compounds is 4-amino-2-chloro benzoic acid. The antibacterial index for *E. coli* was shown by Shive and Roberts (1946) to be related to the enzyme system which synthesizes methionine.

A structural analogue for riboflavin reported to have anti-vitamin activity is isoriboflavin, in which the two methyl groups are in the 5, 6 positions instead of the 6, 7 positions as in the naturally occurring vitamin (Emerson and Tishler, 1944).

Stoerk (1950) used rats and mice to show a severe pyridoxine deficiency produced by the administration of desoxypyridoxine. Symptoms were noted which were not observed in the nutritional diseases that resulted from a pyridoxine-deficient diet.

Woolley and White (1943) reported that the feeding of pyrithiamine to mice caused the characteristic symptoms of thiamine deficiency. This could be cured or prevented by sufficient amounts of thiamine. One molecule of thiamine was required for 40 molecules of pyrithiamine. Eusebi and Cerecedo (1949) noted an effect by pyrithiamine on the food intake of mice overnight. At a ratio of 1: 50 of thiamine: anti-vitamin there was a drop in food intake and loss in weight. Cerecedo, *et al.* (1951) found that 25 moles of neopyrithiamine were required to nullify the action of 1 mole of thiamine in the mouse. Toxic effects were noticed. This compound was more potent than other analogues, and therefore, it was concluded that it was stored in the tissues by

giving a cumulative effect. A study of the mode of action of pyrithiamine by Woolley (1951) showed that it caused inhibition of the synthesis of cocarboxylase from thiamine. It was suggested that it could be a secondary action and that some other function could be primary.

Overman, *et al.* (1942) demonstrated that rats fed dicumarol developed a vitamin K deficiency. Administration of vitamin K overcame the effect.

Preliminary experiments in this laboratory indicated that it was difficult to produce a clear-cut vitamin deficiency in the cockroach, *Periplaneta americana*. Therefore, the purpose of this investigation was to determine the effect of feeding diets which contained an anti-vitamin substituted for the corresponding vitamin.

EXPERIMENTAL

Two or more groups of 14 to 16 nymphs were placed on each diet upon emergence from the egg capsule. Each group was housed in a half-pint jar and reared as described by Sieburth, *et al.* (1951).

The composition of the basal diet was:

Casein (vitamin-free)	30.%
Dextrose	30.
Wesson's Salt Mixture (1932)	4.
Corn Oil	3.
Cholesterol	1.
Cornstarch	32.

In addition each gram of basal diet contained the following vitamins: Thiamine hydrochloride .012 mg., riboflavin .015 mg., niacinamide .100 mg., pantothenic acid .030 mg., pyridoxine hydrochloride .016 mg., inositol 2 mg., biotin .0005 mg., folic acid .005 mg., ascorbic acid .050 mg., para-aminobenzoic acid .050 mg., choline 4 mg., vitamin E .200 mg., vitamin K .025 mg., vitamin A .500 U. S. P. units, vitamin D .400 I. U.

Eleven diets were made up omitting one vitamin and substituting an anti-vitamin in an equimolecular proportion. The following antimetabolites were substituted for the corresponding vitamin:

Niacin:	alpha-picolinic acid[1]
	pyridine-3-sulfonic-acid[2]
	3-acetyl pyridine[2]
Pantothenic acid:	pantoyl taurine[2]
	pantothenol[2]
Para-aminobenzoic acid:	2-chloro-4-aminobenzoic acid[2]
Vitamin K:	dicumarol
Thiamine:	neopyrithiamine[3,4]
Riboflavin:	isoriboflavin[3]
Pyridoxine:	desoxypyridoxine[3]
Folic acid:	4-amino pteroylglutamic acid[5] (aminopterin)

Purina Dog Chow was fed for comparative growth.

[1]Nutritional Biochemicals, 99% pure (1% KCl impurity).
[2]Nutritional Biochemicals, "analytically pure."
[3]Merck and Co., Inc., "analytically pure."
[4]Added at 40:1 molecular ratio. Woolley and White (1943).
[5]Lederle Laboratories Division, American Cyanamid Co., 70% pure.

TABLE I

WEIGHT AND MORTALITY OF NYMPHS AT 30, 60, AND 90 DAYS OF AGE ON CERTAIN VITAMIN DEFICIENT DIETS SUBSTITUTED WITH CORRESPONDING ANTI-VITAMINS

DIET		30 DAYS		60 DAYS		90 DAYS		"t"[1] Values
		Weight mg.	Mortality %	Weight mg.	Mortality %	Weight mg.	Mortality %	
Dog food		37.5	6.7	89.4	10.0	156.6	10.0	2.0
Basal + all vitamins		25.0	6.7	62.5	16.5	105.6	27.2	.....
Deficiency in	Substituted by							
Thiamine	Neopyrithiamine	11.7	10.0	.....	100.0	.....	.....	12.0**
Panthothenic acid	Pantoyl taurine	14.3	20.0	14.5	86.8	.....	100.0	5.6*
	Pantothenol	16.2	23.1	23.9	80.8	.....	100.0	10.9**
Niacin	Alpha-picolinic acid	16.5	12.9	21.0	22.6	26.8	68.6	6.3*
	Pyridine-3-sulfonic acid	15.7	17.4	19.5	30.2	20.2	43.9	2.3[2]
	3-acetyl pyridine	13.9	4.8	17.8	4.8	15.3	33.2	8.1*
Folic acid	Aminopterin	15.3	17.2	33.0	38.0	66.2	44.7	13.1**
P.A.B.A.[3]	2-Chloro-4-Aminobenzoic acid	29.6	3.7	63.0	3.8	100.2	11.0	4.2
Riboflavin	Isoriboflavin	27.5	16.6	59.2	23.3	107.7	36.6	2.1
Pyridoxine	Desoxypyridoxine	28.8	10.7	68.9	14.3	117.9	12.8	1.7
Vitamin K	Dicumarol	33.5	0.0	85.8	0.0	106.4	3.6	4.3

[1]Comparison of growth on diet with basal including all known vitamins at end of thirty days.
[2]8.9 for 60-day growth period, significant at 2% level.
[3]Para-aminobenzoic acid.
*Significant at 5% level.
**Significant at 1% level.

RESULTS AND DISCUSSION

The results of the growth studies and the "t" values are listed in Table I. The "t" values were obtained when the data were analyzed statistically, comparing each diet with the basal ration. The 30-day growth period of the cockroach was used except where otherwise noted.

Using the growth on the basal ration for comparison, the diets containing 2-chloro-4-amino benzoic acid, isoriboflavin, desoxypyridoxine, and dicumarol resulted in similar growth rates, thus possibly indicating that supplements of the corresponding vitamins are not required for the growth of the American cockroach. Noland, *et al.* (1949) also found that para-aminobenzoic acid was not required for growth of the German cockroach, but showed that pyridoxine and riboflavin were required for good growth and survival.

Incorporating alpha-picolinic acid, 3-acetyl pyridine, and pyridine-3-sulfonic acid instead of niacin in the diet of the cockroaches gave depressed growth rates. After 30 days of age there was little or no further growth, although there was no excessive mortality except with the pyridine-3-sulfonic acid group up to 60 days. By 90 days, however, the mortality rate increased markedly for all three groups. Results were fairly comparable with these three analogues. Apparently niacin is required for optimum growth.

Growth rates on the diets containing pantothenol and pantoyl taurine were exceedingly slow and the mortality high. A massive dose of pantothenic acid was given to one group on each diet. They immediately started to gain weight, and mortality ceased. Mortality was 100% by 90 days of age in those groups which were not supplemented. Apparently pantothenic acid is essential for the growth of this insect.

Aminopterin incorporated in the diet in place of folic acid gave a depressed growth rate of about half as much as in the basal ration. Folic acid is, therefore, necessary for optimum growth.

Neopyrithiamine replacing thiamine at a molar ratio of 40: 1 in the diet effectively stopped growth, since none of the nymphs weighed over 12 mg. each at any time. The heavy mortality started at 40 days and by 60 days was 100%. Apparently thiamine is essential for the growth of this cockroach and, with this level of antimetabolite, it is possible that any intestinal synthesis would have been nullified.

SUMMARY

Substituting an anti-vitamin for the corresponding vitamin in a purified diet for the cockroach, *P. americana*, was found to be an effective method for establishing the essentiality of some of the vitamins. The three antimetabolites for nicotinic acid—alpha-picolinic acid, 3-acetyl pyridine, and pyridine-3-sulfonic acid—gave depressed growth rates. Pantoyl taurine and pantothenol caused a similar growth depression in a pantothenic acid free diet but a higher mortality rate.

The most effective antimetabolite was neopyrithiamine, which inhibited growth and caused high mortality when the cockroaches were fed this compound on a thiamine-free diet. Aminopterin (antimetabolite for folic acid) caused a moderate growth depression and mortality rate. In contrast, para-aminobenzoic acid, riboflavin, pyridoxine and vitamin K utilization do not seem to be affected by

their corresponding vitamin analogues. The difference in growth rate of the roaches on basal and dog food ration indicates that there are factors other than those included in the diet which have growth stimulating properties for the cockroach.

ACKNOWLEDGMENT

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TWO NEW SPECIES OF MATUS, WITH A KEY TO THE KNOWN SPECIES AND SUBSPECIES OF THE GENUS (COLEOPTERA: DYTISCIDAE)[1]

FRANK N. YOUNG

The tribe Matini (Dytiscidae, Colymbetinae) is remarkable in having a very disjunct distribution. One genus, *Matus*, is entirely North American; the other *Batrachomatus*, is confined to the Australian region. This, together with the morphological peculiarities of the species, leads to the surmise that the genus *Matus* in the Eastern United States is a relict of a once more extensively distributed group. This idea is further sypported by the extremely local occurrence of some of the species, and by the highly seasonal occurrence of adults, both of which facts seem to indicate a high degree of specialization. Unfortunately, the larvae are practically unknown, and the geological record lacking up until recent or perhaps late Pleistocene times, but even with these impediments, *Matus* presents several interesting problems in variation and geographical distribution. If it is indeed a senescent group a detailed taxonomic study should yield data for comparison with those already derived from studies of more successful, less specialized, and presumably younger genera.

Until H. B. Leech revised the genus in 1941[2] it was thought that only one species, *Matus bicarinatus* (Say), occurred in North America. Leech's work revealed that the widely distributed and relatively rare "*bicarinatus*" is in reality two quite distinct species which are remarkably dissimilar when placed together and compared. The long period during which the second species, *Matus ovatus* Leech, remained unrecognized was probably due to the comparative rarity of the insects in collections, and to undue reliance on the superficial characters which so beautifully demark all the species from the rest of the Dytiscidae.

Shortly after the appearance of Leech's revision in 1941, the writer discovered a very distinct new species of *Matus* in the Apalachicola Flatwoods of western Florida. This form is apparently confined to the flatwoods situations in this rather small region. More recently, through the kindness of Mr. Leech, I have received specimens of another new species from Texas, and upon examining material from other collections found representatives of the species from Arkansas. Both of these new species occur in the Coastal Plain region and their ranges are overlapped by that of *Matus ovatus* without apparent indication of intergradation.

Biometrical and other studies on *Matus ovatus ovatus* and *M. o. blatchleyi* indicate that these forms are actually quite variable and

[1]Contribution No. 482 from the Department of Zoology, Indiana University.

[2]*Can. Ent.*, 73: 77–83, pl. 1, 1941.

show interesting geographical correlations. It is hoped that further work will give a clearer picture of the genus as a whole, but until this study is completed, it seems advisable to publish descriptions of the two disjunct species, and to make available a revised key to the genus. The writer would greatly appreciate information about series of specimens of *Matus* which might be available for study in either private or institutional collections.

Matus leechi sp. nov.

Diagnosis.—The short, broadly ovate form and finely punctate head will readily distinguish this little insect from any of the other species of *Matus*. The male aedeagus (Fig. 2) is distinctive, but similar in general shape to that of *M. bicarinatus*. Average total length about 5.74 mm. (Largest males and females, 5.89 mm.; smallest female, 5.46 mm.). The smallest individuals of *M. ovatus blatchleyi*, the next larger form of the genus, are usually over 7.0 mm. in total length.

Holotype Male.—Ovate, widest slightly behind middle of body. Length, 5.86 mm.; greatest width, 3.11 mm.; width of pronotum at base, 2.73 mm.; width of pronotum at apex, 1.85 mm.; length of pronotum along midline, 1.09 mm.; length of prosternal process, 1.09 mm.; total length of ventral platform, 3.11 mm. *Head:* Microreticulate and finely punctate, the punctures on front between eyes separated by from two to four times their diameter, inconspicuous. Coarser punctures along inner margin of eyes and behind frontoclypeal sutures arranged much as in *ovatus*. Width of head not quite seven-tenths as wide as base of pronotum; width between eyes 1.09 mm. *Pronotum:* Disk microreticulate and finely punctate much as front of head. Series of coarser punctures along anterior margin conspicuous, irregularly distributed; series along base at sides with finer punctures and not reaching to side margins; lateral series originating in anterior angles, but incomplete, not reaching more than about one-third of distance to base. Sides evenly arcuate, the marginal bead distinct but not as wide as terminal antennal segment; anterior angles distinct but not acuminate. *Elytra:* Microreticulate, very finely and irregularly punctate (punctures inconspicuous even at 30x magnification), except for three irregular striae of coarser punctures on each elytron. Tips of elytra almost rounded. *Venter:* Metacoxal plates microreticulate and finely punctate (slightly more coarsely and irregularly punctate than front of head). Prosternal process sulcate almost its entire length. Anterior claw of protarsus not evidently modified, similar to posterior claw. Venter in general similar to that of other species, except for shorter, broader proportions. *Genitalia:* Aedeagus as in Fig. 2; the parameres stouter at tip than in any of the other forms and with the lateral brush of hairs extending along about two-sixths the length of the paramere. *Color:* Dark reddish brown above, the elytra slightly darker on disk with pale margins and head slightly lighter; antennae and legs yellowish brown; venter mostly dark reddish brown, the epipleurae and first abdominal segment lighter.

Allotype Female.—Similar to male, but smaller and somewhat narrower and with the elytral striae a little more conspicuously

impressed. Length, 5.58 mm.; greatest width, 2.94 mm.; width of pronotum at base, 2.65 mm.; width of pronotum at apex, 1.81 mm.; length of pronotum along midline, 1.01 mm.; length of prosternal process, 1.05 mm.; total length of ventral platform, 2.98 mm.; width between eyes, 1.01 mm. Color both above and below somewhat darker than in male, the first abdominal sternite not lighter than others.

Variation.—The series before me is rather uniform in most characteristics varying only slightly in coloration and in size and proportions of body parts. The males average slightly larger than the females in all structures measured as shown in the following table.

	Width of pronotum at Base		Width of pronotum at Apex		Length of prosternal Process		Total Length of Ventral Platform		Total Length	
n	$\bar{x}$	s. d.	$\bar{x}$	s. d.	$\bar{x}$	s. d.	$\bar{x}$	s. d.	$\bar{x}$	s. d.
18♂	2.68	0.06	1.80	0.05	1.08	0.01	3.08	0.08	5.74	0.13
18♀	2.65	0.06	1.80	0.06	1.05	0.01	3.00	0.07	5.67	0.12

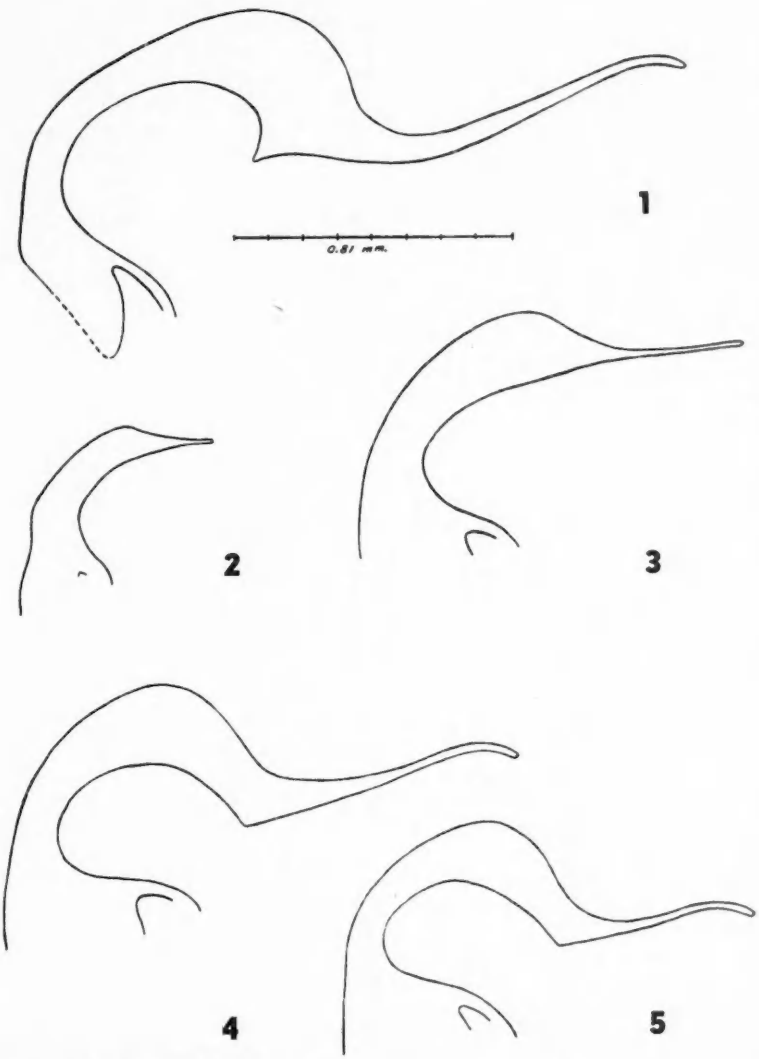
The holotype, allotype, and 49 paratypes are all from Liberty County, Florida (about 6 mi. north of Wilma, T-3-S, R-7-W, Sec. 23) in the Apalachicola National Forest. These specimens were taken in a ditched portion of a swamp stream in the flatwoods. Most specimens were in emergent and submerged vegetation along an undercut portion of bank. Two other paratypes were taken in a stream flowing through a cypress bay (about 5 mi. north of Wilma, same section), where they were found in the leaf axils of a reddish emergent plant (probably a *Juncus*). Three other paratypes are from Gulf County, Florida (about 5.6 mi. east of Gulf-Bay county line near Wetappo), in a swamp stream. The first two collections were made May 2, 1941, the latter on May 3, 1941. Collectors were Dr. and Mrs. Horton H. Hobbs. Jr., Dr. Lewis J. Marchand, and the writer. The highly seasonal occurrence of the adults of this species is indicated by the fact that it was not taken on other trips through this region at other times of the year. Paratypes will be deposited in various museums and the collections of individuals in the United States and elsewhere.

Matus relictus sp. nov.

Diagnosis.—Superficially similar to *Matus ovatus ovatus*, but differing in the structure of the male aedeagus (Fig. 1) and in the narrower, more regularly oval, and attenuate form. About intermediate between *M. bicarinatus* and typical *ovatus* in size and shape; somewhat less convex than either and not at all gibbose in profile. Anterior angles of pronotum distinct to rounded, not acute as in typical *ovatus;* shaped and margined more nearly as in *ovatus blatchleyi* (variable within *ovatus*, western examples tending to have angles rounded or less acute).

Anterior claw of male protarsus relatively shorter and broader than in either *ovatus* or *bicarinatus*, the basal angulation more prominent; not as sharply bent as in *bicarinatus*. Metacoxal plates and last abdominal sternite microreticulate and punctate as in *ovatus*. Average total length about 8.98 mm. (Largest males, 9.18 mm.; smallest males, 8.80 mm.; allotype female, 9.11 mm.)

Holotype Male.—Oval, widest about middle of length, more attenuate behind than typical *ovatus*, but less so than in *bicarinatus*. Sides of elytra not subparallel in basal portion. Length, 9.18 mm.; greatest width, 4.14 mm.; width of pronotum at base, 3.42 mm.; width of pronotum at apex, 2.60 mm.; length of pronotum along midline, 1.54 mm.; length of prosternal process, 1.55 mm.; total length of ventral platform, 4.37 mm. *Head:* Microreticulate and moderately coarsely punctate on front between eyes, the punctures separated by from one to three times their diameter; vertex more finely punctate. Coarser series of punctures arranged much as in typical *ovatus*. Width of head a little more than seven-tenths as wide as base of pronotum; width between eyes, 1.64 mm. *Pronotum:* Microreticulate and moderately coarsely punctate, the punctation on disk finer and sparser than on front of head between eyes. Series of coarser punctures much as in *ovatus;* posterior edge and sides of pronotum with some irregularly vermiculate sculpture. Lateral series of punctures originating at inner base of anterior angles and extending back nearly the whole length of the pronotum to intermingle with the basal series. The lateral series of punctures lie in slight depressions so that the margin of the pronotum above the marginal bead is somewhat protuberant as in typical *ovatus*. Marginal bead similar to that of typical *ovatus*, but turned in at apex of anterior angle. Anterior angles of pronotum distinct, but not acute, similar in appearance to those of *ovatus blatchleyi* or specimens of *ovatus ovatus* from Indiana, Illinois, and Michigan. General shape of pronotum when viewed from above similar to that of *ovatus*, but less narrowed in front. *Elytra:* Microreticulate and less coarsely and densely punctate than front between eyes; punctures not as coarse as in *bicarinatus*, somewhat sparser than in *ovatus*. Microsculpture less impressed (surface more shining) than in many specimens of typical *ovatus*. Series of coarser punctures on elytra arranged as in *ovatus*, but more deeply impressed at base and intermingling posteriorly. Tips of elytra not acuminate, much as in typical *ovatus*. Sides of elytra not subparallel in basal portion. *Venter:* Metacoxal plates microreticulate and moderately coarsely punctate, more finely and sparsely punctate than front between eyes. Prosternal process sulcate nearly its entire length. Anterior claw of protarsus somewhat more than twice as broad, and a little shorter, and more sharply bent at the base than the posterior claw, the basal angulation distinct. Tarsal segments and pads of flat-tipped hairs on fore and middle tarsi much as in *ovatus*. *Genitalia:* Similar in type to those of *ovatus*, but differing in shape and proportions of aedeagus (Fig. 1); parameres similar to those of *ovatus*. *Color:* Reddish brown, with the legs, metasternum and metacoxal plates, epipleurae, first abdominal sternite, head, pronotum, and elytral margins somewhat lighter than disk of elytra and other abdominal sternites.



Drawings of lateral outline of male aedeagi of various species of *Matus*. All drawings were prepared with the aid of an ocular grid and drawn to the same scale on graph paper.

FIG. 1. *Matus relictus* sp. nov. Holotype from Orange, Texas. FIG. 2. *Matus leechi* sp. nov. Holotype from Liberty County, Florida. FIG. 3. *Matus bicarinatus* (Say). Pine, Indiana, April 25, 1911, E. Liljeblad. FIG. 4. *Matus ovatus ovatus* Leech. Paratype from Arlington, Massachusetts, October 25, 1924, P. J. Darlington, Jr. FIG. 5. *Matus ovatus blatchleyi* Leech. Liberty County, Florida (5 mi. north of Wilma), May 2, 1941, F. N. Young.

Allotype Female.—Similar to male, but smaller and slightly darker in color. Length, 9.11 mm.; greatest width, 4.12 mm.; width of pronotum at base, 3.86 mm.; width of pronotum at apex, 2.60 mm.; length of pronotum at midline, 1.59+ mm.; length of prosternal process, 1.69+ mm.; total length of ventral platform, 4.37 mm.; width between eyes, 1.64 mm.

Variation.—The series of specimens before me is rather uniform in size and general shape. All except the holotype, allotype, and one paratype are apparently teneral being light yellowish brown in color.

	Width of pronotum at Base		Width of pronotum at Apex		Length of prosternal Process		Total Length of Ventral Platform		Total Length	
n	*x*	s. d.	*x*	s. d.	*x*	s. d.	*x*	s. d.	*x*	s. d.
7 ♂	3.78	0.12	2.60	0.08	1.54	0.01	4.29	0.09	8.96	0.22
1 ♀	3.86	.....	2.60	.....	1.69	.....	4.37	.....	9.11	.....

The holotype and allotype are from Orange County, Texas, taken at light at Orange, June 20, 1949, by W. C. Stehr (Entomological collection of California Academy of Science). Three male paratypes are from Hempstead County, Arkansas, collected at Hope, June 4, 1926, by Miss Louise Knobel (Calder Collection, University of Michigan Museum of Zoology). Four male paratypes are also from Hempstead County, Arkansas, labelled Hope without other data (Entomological collection of Cornell University).

The following key, amplified from Leech (1941) will serve to separate the described forms of *Matus*. There is considerable variation in size and color within *M. bicarinatus* and *M. ovatus* which probably indicates the existence of subspecies in different geographical regions. The shape of the male aedeagus (Figs. 1–5) is a fairly constant character, however, and should be checked in all cases.

KEY TO THE SPECIES AND SUBSPECIES OF **MATUS**

1. Body form short and broad, not at all attenuate behind; average length about 5.7 mm., (largest males and females, 5.89 mm., smallest female, 5.46 mm.); head finely almost imperceptibly punctate; color dark reddish brown; male aedeagus as in Fig. 2. So far recorded only from the Apalachicola Flatwoods region of Florida ..... **leechi** n. sp.

1'. Body form more elongate, more or less attenuate behind; average size larger (smallest females usually at least 7.0 mm.); head moderately coarsely to coarsely punctate 2

2(1'). Body form elongate oval, attenuate behind; metacoxal plates polished, not microreticulate, sparsely punctate; average length about 8.31 mm. (largest male, 8.75 mm.; smallest male and female, 8.00 mm.); male aedeagus as in Fig. 3. Distribution generally along a line from Massachusetts to Texas; doubtfully reaching northern Florida .. **bicarinatus** (Say)

2'. Body form more evenly ovate, not very attenuate behind, or if so with sides of elytra subparallel in basal portion; metacoxal plates microreticulate (hard to see, particularly in teneral specimens) and punctate ... 3

3(2'). Body form less strongly ovate, broadest about middle of length, narrower in proportion to length; average length about 8.98 mm. (largest males, 9.18 mm., smallest, 8.80; allotype female, 9.11 mm.); male aedeagus as in Fig. 1. Texas and southern Arkansas..... **relictus** n. sp.

3'. Body form often strongly ovate, broadest behind middle of length; sides of elytra often subparallel in basal portion; male aedeagi as in Figs. 4 and 5..... 4

4(3'). Average length greater, about 8.5 mm. (7.5 to 9.4 mm.); general color brownish red, the elytra slightly darker; anterior angles of pronotum acute to rounded (acute in typical specimens from Massachusetts); metacoxal plates more coarsely and closely punctate. Range from Ontario and Quebec south to Maryland, Indiana, and Illinois (doubtfully recorded from Mobile, Alabama)..... **ovatus ovatus** Leech

4'. Average length less, about 8.0 mm. (7.0 to 9.1 mm.); general color dark reddish brown to piceous, the elytra usually much darker, the pronotum usually lighter; anterior angles of pronotum rounded; metacoxal plates usually very finely and sparsely punctate. Range from southern Florida to Georgia, southern Alabama, and eastern Texas..... ..... **ovatus blatchleyi** Leech

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HOMOPTERA, FAM. MEMBRACIDAE, by W. D. FUNKHOUSER. Genera Insectorum, Fasc. 208. Pp. 383, 14 pl., 9 text figs., 1951.

This monumental contribution to the systematics of this family finally has been published. It represents the greatest contribution to the long series of studies of this family made by Dr. Funkhouser. Unfortunately, the manuscript was sent to Europe before World War II, but was not published until recently. Fortunately, however, the manuscript and the plates escaped the ravages of war. The plates were originally painted in colors but have been reproduced in black and white. Many details have been lost by this process. This suggestion is not offered as a criticism but as a simple statement of fact. Neither is it intended as a statement which might detract from the usefulness of such illustrations as an aid in interpreting the characters used in keys and descriptions. There is another general statement which should be made. The classification is substantially that of Funkhouser's catalogue published in 1927. Considerable advances have been made in the classification of the family during the last 25 years, notably the later work by Goding. Perhaps many of the contributions were published after the manuscript was completed.

There is a general introduction devoted to such subjects as characters, phylogeny, distribution, habits, mimicry, attendance by ants, external anatomy, internal anatomy, life histories, hosts, enemies, and economic importance.

The main portion of the book is devoted to classification. A key to the subfamilies recognizes the six commonly accepted. Each of these subfamilies then follows a general pattern with a key to the tribes, each tribe with a key to the genera. Each genus is followed by the original reference and also the original reference for the synonyms, if any. This is followed by a description of the genus with a genotype designated. Then follows a catalogue of the species and their known synonyms with indications of the known geographic distribution. Unfortunately, only the original references for genera and species are given, whereas in most cases subsequent references are of vastly greater importance. It is unfortunate that these important items could not have been included. Fortunately, there is available for the serious student Funkhouser's Catalogue and the later works of Goding.

The format, the printing, and the paper seem to be excellent, although the size of the page in Genera Insectorum is too large to be convenient. Typographical errors are few and of no serious import.

It is greatly to be regretted that Dr. Funkhouser did not live to see in its printed form this his final and greatest contribution to his long series of papers.

—Z. P. METCALF.

TERMINOLOGY OF THE PRETARSUS[1]

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It is often the case in Entomology, as well as the other sciences, that authors, not realizing a specific structure has been previously named and described, create another homonym or synonym. Only through searching the literature is one able to discover the many confusing and interchangeable terms that have been used for a structure, and, unfortunately, this also applies to the pretarsus. With the growth of the pretarsus as a taxonomic unit of definite value, and the increased interest in the physiology of the pretarsus, a stable terminology is necessary. Hence, it is my desire that the following glossary will bring order from the chaos in which the terminology of the pretarsus now exists.

Those terms in bold face are those that should be continued in general practice and should be standardized. The terms were selected for the following reasons: (1) to eliminate homonyms (a homonym in Entomology is a term that is identified with more than one part of the insect body, for example, the digitus) and synonyms; (2) weight of usage, for example, the term "unguitractor plate" is grammatically incorrect, because it is a case of a noun modifying a noun, therefore, unguitractor*ial* plate should replace unguitractor plate, but because of its common usage, unguitractor plate is retained; (3) the term is universal, *i.e.*, homologous in several hexapod orders.

The more important structures of the pretarsus are illustrated on Plate I.

Adhesive organ (Snodgrass 1925), *Haftapparat* (Arnhart 1923): The adhesive organ is that part of the pretarsus exclusive of the claws, and includes the arolia, pulvilli, unguitractor plate, and any other structures which may be present. It arises between and below the base of the claws, and enables the insect to cling and walk on smooth surfaces.

Apodeme: See **unguitractor tendon.**

Arolanna: See **arolium.**

Arolella: See **pseudarolia.**

Aratendon: See **unguitractor tendon.**

Arcus (Snodgrass 1942), *camera* (MacGillivray 1923), *Bow* or *Bugel* (Arnhart 1923): In 1942 Snodgrass chose to call what MacGillivray had previously designated the *camera*, the *arcus*. Although both terms refer to arched structures, arcus is the better of the two, because there is no confusion for describing the function of the eye and a morphological structure. The arcus is the sclerotized structure supporting the proximal area of the arolium or arolia.

Aroliar Manubrium: See **orbicula.**

Arolium, *arolanna, artarolium* (MacGillivray 1923), *empodium, onychium, pulvillus:* The arolium is the median pad-like or setiform structure between the bases of the claws, which alternate with the unguifer. Crampton (1923) points out that the arolium has been more widely studied by the "students of the lower groups,"

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[1]Contribution from the Entomology Laboratory of the University of Illinois.

[2]This work is a portion of a thesis required in partial fulfillment of a Master of Science degree in Entomology at the University of Illinois. I would like to extend my appreciation to Professor W. P. Hayes, under whose direction this work was carried out.

but whether it is the median structures of the Hymenoptera, Lepidoptera or Trichoptera (Holway 1935), it should be referred to as the arolium. The arolium is the median terminal lobe of the pretarsus, or insect foot (Torre-Bueno 1950). Smith (1906) erroneously called the arolium "one of the lobes of the pulvillus." Levereault (1935) says that *arolium* is Latin "for a roll of cloth," and suggests the term *pulvillus*, which means "pads" (Melander 1940). It must be admitted that arolium is a poor choice, but so many other terms have been used for the pulvillus that a change would add to the chaos. *Arolanna* (MacGillivray 1923) is a special name for the arolium of the Hymenoptera where it resembles the pseudarolia.

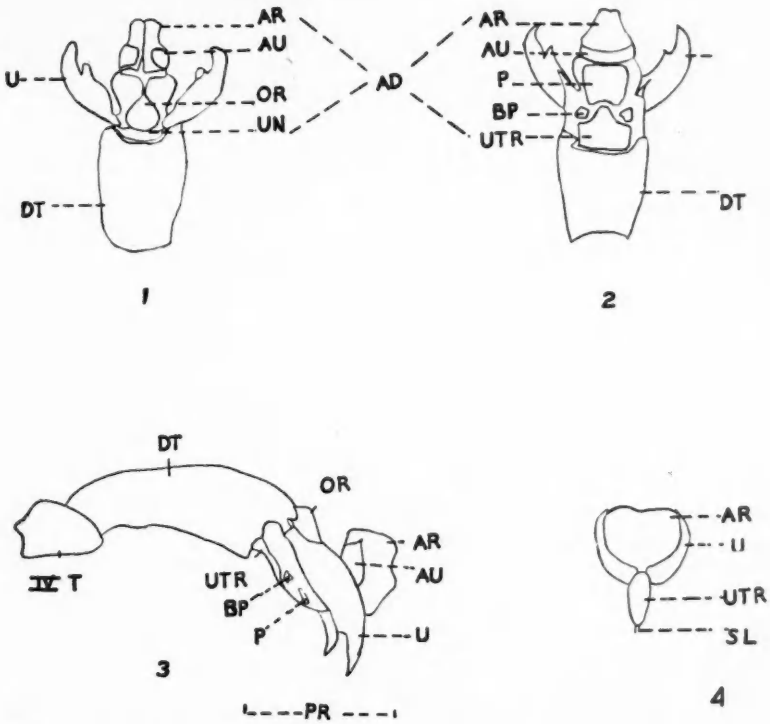

FIG. 1. Dorsal aspect of the pretarsus of the honeybee devoid of vestiture. FIG. 2. Ventral aspect of the pretarsus of the honeybee destitute of vestiture. FIG. 3. Lateral aspect of the pretarsus of the honeybee without vestiture. (Redrawn from Snodgrass, 1925. Terminology mine.)

FIG. 4. Ventral aspect of pretarsus of hind leg of *Tettigonella lineata* Sign., no vestiture. (Redrawn from Fennah, 1945.)

LIST OF ABBREVIATIONS

AD = adhesive organ
AR = arolium
AU = arcus
BP = basi pulvillus
DT = distitarsus
OR = orbicula
P = pulvillus
PR = pretarsus
SL = sublinear plate
U = ungues
UN = unguifer
UTR = unguitractor
IV T = tarsal subsegment

Aroliodea: The coria (=membrane between the body segments and subsegments of insects) at the distal end of the tarsus that forms a distended bag in some Hemiptera (MacGillivray 1923). I have not seen the structure Dr. MacGillivray calls the aroloidea in my work.

Artarolium: See **arolium.**

Articularis: See **pretarsus.**

Auxilla: See **basipulvilli.**

Auxillary plate: See **basipulvilli.**

Basipulvilli, *auxilliae, auxillary plate*: MacGillivray (1923) used this term for the Hymenoptera, but it can also be applied to all orders. The basipulvilli are small plates at the proximal region of each pulvillus, or at the base of the claws when the pulville are present. "They may extend laterally around the base of the claws" (Crampton 1923).

The term *basipulvilli* is descriptive, and therefore its function identified. When first looking at the term auxillary plate or auxilliae, the student is apt to be reminded of the axillary sclerites or axillaries. Hence, the preference for the term basipulvilli rather than auxilliae.

Bow: See **arcus.**

Bugel: See **arcus.**

Calcanea: See **unguitractor plate.**

Camera: See **arcus.**

Claws: See **ungues.**

Condyle: See **unguifer.**

Dactyl: See **dactylopodite.**

Dactylopodite, *dactyl, dactylus, digitus, distitarsus:* The dactylopodite is the seventh segment of the generalized arthropod leg, and it is homologous with the pretarsus. Smith (1906) says that this structure is a "finger or toe: a tarsal joint after the first one, when that is enlarged in bees." The term digitus refers to the distitarsus, a small appendage attached to the lacina, and a finger-like lobe of the male genitalia or Lepidoptera.

Depressor of the claws: See **retractor muscle.**

Digitules: See **tenent hairs.**

Digitus: See **dactylopodite.**

Distitarsus, *digitus, onychium, pretarsus* (Levereault 1935), *ungula:* The distitarsus is the terminal, or most distal tarsal segment, although Levereault (1935) prefers to call it the *pretarsus*, and Torre-Bueno is of the same opinion when he says it is the "last segment of the tarsus, bearing the ungues." I am inclined to agree with Crampton (1923) who states, "the distal segment of the tarsus may be termed the distitarsus, since the term onychium, which is also used for the arolium, empodium, and other structures, and it is impossible to determine the original or most widespread use of the term onychium. . . . The term digitus, ungula, etc., are also loosely applied to the distitarsus by some investigators."

Empodial hairs: See **parempodia.**

Empodium, *arolium, onychium, paronychia, planta* (Lowne 1890–2), *process plantaris* (de Meijere 1901), *pseudonychia, pulvillus, Trittborste, unguiculus:* "As for the term 'empodium,'" says Levereault, "it is not needed, since it is recognized by most morphologists as an elongated process of the unguitractor. It is hardly sensible to have two terms for one structure." But the term *empodium* has nine synonyms. Even though the empodium is not always present, and it varies in shape and form so that it has taxonomic value, how can the morphologist and taxonomist refer to an unnamed structure? The confusing array of terms applied to the empodium is sufficient to make one senseless; therefore, the term should be defined, and the controversy settled.

Maynard (1951) in his monograph on Collembola, states that the unguiculus is equal to the empodium or empodial appendage. Holway (1935) points out, it is erroneously associated as the pulvillus. Smith (1906) defines the empodium as "a bifid pseudotarsi between the claws" of Coleoptera. The empodium is a true median anterior process of the unguitractor plate that does not articulate with the unguifer, may be lobed or spine-like, and the spine may be setose.

Euplantulae, *planta, plantula, pulvillus, pulvinis* (MacGillivray 1923), *tarsal pulvillis, sole:* The euplantulae are pad-like structures on the ventral surface of the tarsal subsegments; they are especially noticeable on the grasshopper. The euplantulae are not the pulvilli. There is a possibility of misinterpretation between the words *planta, plantula*, and *plantagrade:* therefore the term

euplantula is preferred. In 1925 Snodgrass said that they are sometimes called *tarsal pulvilli*. Another example of terminological synonymy is the pulvinis of MacGillivray. He defines the *pulvinis* as the surface of the tarsal subsegments which bear tenent hairs.

Flexor membrane: The membrane surrounding the claws which makes the claws move when tension is transferred from the unguitractor tendon to the unguitractor plate to the membrance. It has also been suggested that this is the area from which the pulvilli developed (Holway 1935).

Flexor muscle: See **retractor muscle.**

Gelenkhocker (de Meijere 1901): See **unguifer.**

Gleitrinne or *Gleitflache* (de Meijere 1901): See **plantella.**

Haftlappchen: See **pulvillus.**

Krallenglied: See **pretarsus.**

Manubrium: See **orbicula.**

Onyches: See **unguifer.**

Onychii: See **ungues.**

Onychium: See *arolium, claw, distitarsus, empodium, nail, pulvillus:* Hayes and Kearns (1934) say that the term *onychium* is used for the distitarsus in certain of the Hymenoptera. MacGillivray (1923) defines it as the distal end of the calcanae (=unguitractor), and prolongs into a slender knob. MacGillivray's definition is a description of the empodium. Torre-Bueno (1950) states that it is "a nail, claw, small processes between the tarsal claws in many Diptera." In Hymenoptera they are apical claw bearing joints. (Smith). Holway (1935) explains, and I agree with his opinion, that it is "used in such a variety of ways that it appears impossible to define satisfactorily"; therefore, I recommend that its use be discontinued.

Orbicula, *aroliar manubrium, manubrium* (Snodgrass 1942), *Stutzplatte* (Arnhart 1923): The orbicula is a sclerite on the dorsal surface of the pretarsus, at the base of the arolium, and distad of the unguifer between the claws; it is not always present. In 1942, however, Snodgrass called the orbicula the *manubrium*, or *aroliar manubrium*. The term *manubrium* also refers to "that part of the mesosternum in Elateridae which forms the process for fitting into the cavity of the prothorax; in Colembola, the large median base of the furcula." Hence I would recommend the use of the term *orbicula* instead of *manubrium*.

Note the spelling of this term, *orbicula*, and of *orbicular*, which is a round or oval spot situated in the discal cell of Lepidoptera (Comstock 1924).

Palmula: See **pulvillus.**

Parempodia, *empodial hairs, paronychia, tasthaare, unguitractor setae* (Crampton 1923): The parempodia are the apical setae, or bristle-like appendages of the empodium. There may be one or two. The parempodia should not be mistaken for the tenent hairs of the Coccidae which MacGillivray calls the digitules. Parapodium is an appendage of the Symphyla (Comstock 1924), pseudopods or parapods are appendages of dipterous larvae and they should not be confused with *parempodia*. If the onychium is considered as the empodium, then the paronychia is the bristle-like appendage of the onychia. For the reasons stated by Crampton in 1923, I am not continuing the use of the term *onychium*; therefore, the term *paronychia* falls into disuse also.

Paronychium: See **parempodia.**

Parapulvillus: See **pulvillus.**

Planta, *euplantulae, plantar, plantulae, scopa, sole* (Arnhart), *solea* (MacGillivray), *unguitractor:* Lowne (1890–2) described the unguitractor and empodium of *Calliphora erythrocephala* (Diptera: Calliphoridae), but incorrectly calls them the *planta*. Arnhart's *sole* is a sclerite on the median ventral surface of the pretarsus, distad to the unguitractor, and between the claws. Actually, Arnhart's definition is an excellent description of the planta. Snodgrass (1925) hypothesized that the planta may be a subdivision of the unguitractor. In lepidopterous larvae the planta is the distal portion of the proleg on which the crochets are borne (Peterson 1948). Unfortunately, the pollen combs of Apoidea on the inner surface of the metatarsus (=first tarsal segment) is also called the *planta* (Comstock 1924). The term *scopa* (Latin, broom) is a more precise term for the pollen gathering combs. *Plantar* refers to the sole of the foot.

Plantar: See **Planta.**

Plantar surface: The surface of the tarsi applied to the ground in walking. "In general the lower surface of the tarsus," (Torre-Bueno).

Plantella, *Gleitrinne* or *Gleitflache* (de Meijere 1901): MacGillivray named "a long median projection of the last tarsal segment" the *plantella*. The *Gleitrinne* or *Gleitflache* of de Meijere are the set form prolongations of the ventral wall of the distitarsus. For all intents and purposes, de Meijere and MacGillivray's definitions are the same; therefore let us retain the more definitive term, *plantella*.

Plantigrade: Those insects which walk on the entire tarsi, including the pretarsus, are known as plantigrade walkers (Torre-Bueno).

Pr(a)etarsus, *articularis, dactylopodite, distitarsus, Krallenglied (Arnhart), posttarsus* (MacGillivray), *transtarsus* (Hansen 1930), *ungues, ungula* (Schiodte):[3] The pretarsus is the sixth segment of the insect leg, which bears either one or two claws and the adhesive organ. The pretarsus may be partly retracted in the distal part of the distitarsus. In Collembola it is the "small apical distal part or transtarsus" (Mills 1934). However, Hansen (1930) prefers to use the term *transtarsus* for all orders, since *pre* signifies before and *trans* signifies beyond. When de Meijere first named the sixth segment of the insect leg the *praetarsus* (angelicised to *pretarsus*), he made it clear that he would not call the pretarsus *protarsus*, because *pro* would indicate prothorax and confusion would exist. The dactylopodite is the corresponding segment in other arthropod legs, *e.g.*, Diplopoda and Arachnida. MacGillivray disagreed with the term *articularis* used by some authors, hence he suggested *posttarsus*. The common use of the term *pretarsus* will make it difficult to use the more logical *posttarsus* in its place.

Pseudarolia (Knight 1941), *arolella* (MacGillivray): The cusion or flaplike membranous area attached to the claws itself "may be very hairlike or membranous" (Knight) is the pseudarolia. They may be found beneath the claws in Hymenoptera. The bladder-like portion is sometimes attached to the minute proximal sclerite, the ungulis" (MacGillivray).

Pseudoempodium: Crampton in 1923 identified a median bristle-like structure between the base of the claws as the pseudempodium. This is not the empodium, because the empodium is distad of the unguitractor.

Pseudonychia, *empodium, paronychia:* are lateral teeth on the ungues of Collembola (Mills 1934).

Pulvicorium (MacGillivray): is the coria in the distitarsus on each side of the unguifer, and may be produced into a long slender tail-like lobe, which may be as long as or longer than the claws. Each lobe is known as a *pulvicoria*, and may be pectinate. One should be careful not to mistake this term for the plantella, which is not the coria but is a projection from the distitarsus.

Pulvillus, *arolanna, arolium, euplantulae, Haftlappchen, pamula* (Smith), *onychii, onychium, parapulvillus, tulillus* (MacGillivray): The pulvilli are the pad-like structures on either side of the unguitractor plate, and they are usually closely associated with the ventrobasal region of the claws. MacGillivray restricts the term pulvillus to the Diptera, and unfortunately substitutes the word *tulillus* for it. The euplantulae or tarsal pulvilli refer only to the ventral pads of the tarsal subsegments. Levereault (1935) says, "It is here acknowledged that the term pulvillus has been used for the paired pads beneath the claws of certain insects, but since these paired pads are not probably ventrolateral evaginations of the median pulvillus (=arolium) why is not the term parapulvillus better for the pad beneath the claws?" No, because if we continue to rearrange and supplant terms in common use, for new terms, although they may be more meaningful, disorder will continue to exist.

Crampton has offered two possibilities for the development of the pulvilli. They are: (1) In some Hymenoptera a portion of the arolium is divided by a deep furrow. Certain Hemiptera and Homoptera have a suggestion of the arolium dividing into two lateral regions. The pretarsus of some asilid flies have both, a pair of pulvilli and an arolium, which gives further indication that the pulvilli are detached portions of the arolium. (2) The other hypothesis claims that the pulvilli may have developed from the membranous areas of the claws, for example, the pulvillus and its relation to the basipulvillus in the cockroach. Some ephemerids have pad-like claws which lends weight to the view that the pulvilli are a detached portion of the claw which becomes cleft.

Retineria: See **tenent hairs.**

Retractor of the claw: See **unguitractor.**

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[3]Information on the observations of Schiodte were obtained from quotations.

Retractor muscle, depressor of the claw, flexor muscle: The muscle acting upon the unguitractor tendon to pull the unguitractor plate.

Sehne: See **unguitractor tendon.**

Sole: See **planta.**

Stutzplatte: See **unguitractor.**

Sublinear Plate (Fennah 1945): The proximal margin of the unguitractor is "connected to a sublinear plate from which a long thread-like tendon passes through the leg." My observations with the Hemiptera do not indicate any such structure. At the point of origin of the tendon, from the base of the unguitractor plate, the tendon widens and assumes a triangular shape. Most likely this is the deviation of the unguitractor tendon that Fennah calls the sublinear plate. It would be well to investigate and see if the sublinear plate of the Homoptera is the same triangular shaped area of the Hemiptera unguitractor tendon or other orders.

Tarsal claws: See **ungues.**

Tarsule: See **ungues.**

Tarsulles: See **ungues.**

Tasthaare: See **empodium.**

Tarsungulus (Peterson 1950): "The terminal claw-like segment of the leg of many coleopterous larvae found by fusion of the tarsus and the claw."

Tendon: See **unguitractor tendon.**

Tenent hairs, *digitules* (MacGillivray), *retineria:* Smith (1906) called them "appendages on the feet of Coccidae," and they usually number from two to four (Smith). The retineria of MacGillivray are small microscopic setae-like projections on the ventral part of the tarsi that secrete a sticky substance. *Tenent* refers to holding or clasping, and tenent hairs are hairs that are used to hold or clasp something, or aid in adhering to surfaces. Tenent hairs are small setae that usually form a dense mat over the planta and euplantulae. Their tips are expanded and they secrete a substance.

Tubercula: See **unguifer.**

Tulillus: See **pulvillus.**

Ungues, claws, *onyches, onychii, tarsal claws, unguicula:* The claws are usually referred to as the *ungues:* they are at the distal end of the pretarsus. In Corixidae the unguicula refers to the single claw of the palea.

Unguicula: The unguicula is the smaller of the two tarsal claws of the Collembola. It also is used by Griffith (1945) to mean the single claw of the palea.

Unguifer, *condyle, Gelenkhocker* (de Meijere), *tubercula* (MacGillivray): The unguifer is the dorsal sclerite at the distal end of the distitarsus which the ungues (=claws) articulate. The term condyle is not preferred because it is, in one case, a process which articulates the base of the mandible to the head. We assuredly do not want to mistake the foot for the head.

Unguiflexor tendon: See **unguitractor tendon.**

Unguis: The larger of the two claws on the Collembola pretarsus. It is applied to a short process on the sixth antennal joint in some aphids (Smith 1906). Kirby and Spence (1846) employ the term for the claw-like structure of the maxilla.

Unguitractor, *calcanea, flexor plate, retractor, Stutzplatte, tarsule, tarsulus, unguitractor plate:* The unguitractor is the most constant structure of the pretarsus, besides the claws. It is on the ventral surface of the pretarsus posterior to the claws and from its base the unguitractor tendon arises. The unguitractor is of taxonomic value.

Unguitractor setae: See **parempodia.**

Unguitractor tendon, *apodeme, aratendon, Sehne, tendon, unguiflexor tendon, unguitractor:* "There are really no true tendons in insects, **i.e.,** the tendons of the legs are only such in a physiological or morphological sense, and not at all in structure or origin. . . . The only differences between a skeletal process and a tendon is that one is invaginated from a relatively fixed part of the body and the other from a moving part. While insect tendons are, therefore, not homologous with the tendon of vertebrates, it is probably wise to retain the name just as in the case of the femur and tibia for parts of the leg." This is taken from Woodworth (1908) and his opinion is still valid.

Ewing (1928) and others have shown that, originally a muscle did have its origin at the base of the unguitractor, and now the unguitractor tendon is in its place. A fine example is the Corixidae. Korschelt (1938) demonstrated that an invagination of hypodermal cells over the muscle produces the insect

tendon. Hence, the use of the term *apodeme*, which is an ingrowth of the body wall, is incorrect since it does not consider the overgrowth of muscle tissue by hypodermal cells. The aratendon of MacGillivray is the unguitractor. The unguitractor tendon arises from the base of the unguitractor and extends to the coxa (Hayes & Kearns) and branches in the tibia where it gives off a muscle and another in the femur.

Ungula: See **ungues.**

Ungules: "The bladder-like portion (or the pseudarolia) is sometimes attached to a minute proximal sclerite the ungules" (MacGillivray 1923).

I believe that these are all the terms related to the pretarsus, but there may be others that I have neglected in other publications.

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FURTHER STUDIES[1] ON THE MODE OF ACTION OF ORGANIC THIONOPHOSPHATE INSECTICIDES

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Recent studies by Diggle and Gage (1951) and by the authors (1952) have shown that highly purified parathion and certain other thionophosphate insecticides are poor inhibitors of the cholinesterase enzymes *in vitro*, and that the inhibitory actions widely described in the literature (DuBois, *et al.*, 1949, Metcalf and March, 1949, Grob, *et al.*, 1950, Aldridge, 1950, and Giang and Hall, 1951) are probably due to traces of isomerides, such as O,S-diethyl O-*p*-nitrophenyl thiophosphate, which are formed very readily by heating during reaction or distillation, by ultraviolet radiation, or even by long standing at room temperature and in light. These isomerides are nearly as active *in vitro* inhibitors of cholinesterases as are the corresponding oxygen analogues of the thionophosphates, such as para-oxon (diethyl *p*-nitrophenyl phosphate) and are from 1000 to 10,000 or more times as active as the purified thionophosphates. Therefore the presence of the isomeride in the thionophosphate in traces as low as 0.01 per cent will produce appreciable cholinesterase inhibition at dilutions of the order of 10^{-6}M such as have been generally credited to parathion.

Since it can be shown that purified thionophosphates are lethal to insects (and mammals) by progressive *in vivo* inhibition of central nervous system cholinesterase (Table I) and that the LD_{50} values for the thionophosphates are virtually equivalent to those of the corresponding phosphates (Metcalf and March, 1949), it is evident that some metabolism of the thionophosphates to active anticholinesterases must occur in animal tissues. The most reasonable assumption would appear to be that the thionophosphates are transformed *in vivo* to the much more active phosphates according to the following equation:

$$O_2NC_6H_4O\overset{\overset{S}{\|}}{P}(OEt)_2 \xrightarrow[\text{enzyme}]{O_2} O_2NC_6H_4O\overset{\overset{O}{\|}}{P}(OEt)_2 + SO_4^-$$

Such transformation can be easily accomplished in the cold by oxidation with nitric acid (Giang and Hall, 1951). This possibility, which has been suggested by Grob, *et al.*, 1950, is in good agreement with the

[1]This paper is the fourth of a series dealing with the mode of action of organic phosphorus insecticides.

observation that at equal dosages the time required to produce comparable toxic effects in flies is about 3 to 5 times as long for parathion as for para-oxon (Metcalf and March, 1949). Chamberlain and Hoskins (1951) attempted to demonstrate this conversion by incubating parathion with insect blood, muscle, fat body, digestive tract, or integument from *Periplaneta americana* (L.), but were unable to produce a more active compound in *in vitro* tests. Incubation with the intact nerve cord for several hours, however, produced evidence of activation. Diggle and Gage (1951) have very recently reported that mouse liver can also produce activation to a more active anticholinesterase.

TABLE I

In Vivo INHIBITION OF FLY BRAIN CHOLINESTERASE BY TOPICAL APPLICATION OF APPROXIMATE LD_{99} OF PURIFIED THIONOPHOSPHATES

Compound	Topical Dosage in γ Per Gram Female Fly	Time Symptoms	Per Cent ChE Inhibition. Average of 15 Brains
O,O-dimethyl O-*p*-nitrophenyl thionophosphate	2	4 hrs.—agitated....	84
		6 hrs.—prostrated	90
O,O-diethyl O-*p*-nitrophenyl thionophosphate	2	2 hrs.—agitated, some down.....	49
		4 hrs.—prostrated	75
O,O-diisopropyl O-*p*-nitrophenyl thionophosphate	10	4 hrs.—agitated....	74
		6 hrs.—prostrated	82

This paper provides data to show that such a conversion of the thionophosphates to active cholinesterase inhibitors readily occurs in the presence of mammalian and insect tissues, under appropriate conditions, and reports studies of the mechanism of this conversion.

MATERIALS AND METHODS

The organic thionophosphate esters used in this study were highly purified in order to eliminate traces of the S-alkyl isomerides, which have been mentioned as highly active anticholinesterases. The compounds studied include O,O-diethyl O-*p*-nitrophenyl thionophosphate (parathion) 99.8 + per cent pure,[2] a colorless nearly odorless liquid, melting about 6° C., $n_D^{20°} = 1.5384$; O,O-dimethyl O-*p*-nitrophenyl

[2]Obtained through the cooperation of Dr. J. L. Horsfall of the American Cyanamid Corpn.

thionophosphate (methyl parathion) m.p. 36–7° C.[2], and O,O-diisopropyl O-*p*-nitrophenyl thionophosphate, m.p. 56–7° C.[2], both white, odorless solids recrystallized four times from ethyl alcohol; O,O-dimethyl S-(1,2-dicarbethoxyethyl)-dithiophosphate (malathon), 99+ per cent pure,[2] a colorless liquid, $n_D^{20°} = 1.4991$, with a faint sulfurous odor; O,O-diethyl S-carbamyl methyl dithiophosphate, a white solid, m.p. 61–2° C.[2]; and ethyl *p*-nitrophenyl thionobenzenephosphonate (EPN) m.p. 35–6° C., a white nearly odorless solid,[3] recrystalized six times from petroleum ether. Methyl parathion was used in most of the experiments because of the ease of its purification in relatively large amounts and the convenience in handling a solid. Standard solutions of these materials in acetone or alcohol were stored in the refrigerator to prevent isomerization by heat and light.

The cholinesterase determinations were made manometrically at 37° C. (Metcalf and March, 1949) using a brei of 3 female house fly heads per ml. of buffer solution. Acetyl choline bromide was used as the substrate at 0.01 M. The inhibitors were added in 0.1 ml. aliquots in alcohol or acetone. Activities were determined over a 30-minute period, following 10 minutes preliminary equilibration and were compared with an unpoisoned standard to determine the per cent inhibition of the enzyme. In the experiments involving tissue incubation, the mouse liver slices and various organs of the American cockroach, *P. americana* (L.), were placed in 2.8 ml. of Krebs-Ringer phosphate buffer solution (Umbreit, *et al.*, 1949), pH = 7.4, containing 0.01 M. glucose, and the flasks were oxygenated for 5 minutes. The phosphorus compounds were added to the incubation medium in 0.1 ml. aliquots in ethyl alcohol and additional inhibitors, if required, in 0.1 ml. aliquots in water or acetone. The final volume was in all cases 3 ml.

RESULTS

Table I shows that the highly purified thionophosphates, although previously shown to be of very low activity as anticholinesterases *in vitro*, produced marked inhibition of the central nervous system of *Musca domestica* L., when topically applied in doses approximating the LD_{99}. The intensity of the cholinesterase inhibition was correlated with the severity of the symptoms, as previously reported for the honey bee (Metcalf and March, 1949).

Production of anticholinesterase from thionophosphate substrates by tissue incubation.—Mouse liver slices of 30 to 100 mg. dry wt. or the digestive tracts of *P. americana* were immersed in the modified Ringer

[3]Obtained through the cooperation of Dr. S. S. Sharp of the E. I. duPont de Nemours Inc.

solution to which were added ethyl alcohol solutions of several purified thionophosphates to give concentrations ranging from 3.3×10^{-5} M. to 1×10^{-2} M. depending upon the purity and anticholinesterase activity of the thionophosphate sample. The final volume was 3 ml. and the reaction was carried out in Warburg vessels at 37° C. After shaking for 1 hour in the presence of oxygen, 0.3 ml. of the fluid in the flask was removed and added to another flask containing 2.4 ml.

TABLE II

CONVERSION OF THIONOPHOSPHATES TO ANTICHOLINESTERASE BY INCUBATION WITH TISSUE FOR ONE HOUR AT 37° C.

Compound	Tissue	Concentration for ChE Assay Molar	Per Cent Fly Brain ChE Inhibition
O,O-dimethyl O-*p*-nitrophenyl thionophosphate	None	3.3×10^{-5}	0
O,O-dimethyl O-*p*-nitrophenyl thionophosphate	Cockroach gut	3.3×10^{-5}	99
O,O-dimethyl O-*p*-nitrophenyl thionophosphate	Mouse liver slice (134 mg. dry wt.)	3.3×10^{-5}	91
O,O-diethyl O-*p*-nitrophenyl thionophosphate	None	3.3×10^{-5}	5
O,O-diethyl O-*p*-nitrophenyl thionophosphate	Cockroach gut	3.3×10^{-5}	96
Ethyl *p*-nitrophenyl thionobenzene phosphonate	None	3.3×10^{-6}	19
Ethyl *p*-nitrophenyl thionobenzene phosphonate	Cockroach gut	3.3×10^{-6}	99
O,O-diethyl S-carbamyl methyl dithiophosphate	None	1×10^{-3}	21
O,O-diethyl S-carbamyl methyl dithiophosphate	Mouse liver slice[5]	1×10^{-3}	67
O,O-dimethyl S-(1,2-dicarbethoxy ethyl) dithiophosphate	None	3.3×10^{-5}	91[6]
O,O-dimethyl S-(1,2-dicarbethoxy ethyl) dithiophosphate	Cockroach gut	3.3×10^{-5}	96
O,O-dimethyl S-(1,2-dicarbethoxy ethyl) dithiophosphate	None	3.3×10^{-6}	34
O,O-dimethyl S-(1,2-dicarbethoxy ethyl) dithiophosphate	Cockroach gut	3.3×10^{-6}	73

[5]Two hours incubation.

[6]This concentration gave 34 per cent ChE inhibition when added immediately to the fly brei without 1 hour incubation.

of house fly brain brei and 0.3 ml. of 0.1 M. acetylcholine bromide in the side arm resulting in a final volume of 3 ml. The anticholinesterase activity of the solution which then contained one-tenth the original concentration of thionophosphate (assuming no change) was measured. The results obtained are given in Table II. With the unincubated thionophosphate no appreciable inhibition was obtained,

except in the case of O,O-dimethyl S-(1,2-dicarbethoxyethyl)-dithiophosphate which was apparently slightly impure. However, with the solutions incubated with either the mouse liver slices or roach digestive tract, a high degree of cholinesterase inhibition occurred, indicating the production of compounds with high inhibitory activity.

In order to be able to relate various degrees of cholinesterase inhibition produced by the unknown inhibitor, the inhibition resulting from the addition of various amounts of a 3.3×10^{-4} M. solution of methyl parathion incubated 1 hour with known weights of tissue was measured. When these values were corrected to 100 mg. dry weight of tissue and plotted as logarithm of ml. of solution concentration vs. per cent inhibition, the straight line curve of figure 1 resulted. Using this curve, it is possible to express any per cent cholinesterase inhibition obtained with methyl parathion in terms of ml. of solution of metabolized methyl parathion produced per hour per 100 mg. tissue. Such values were subsequently used to compare the activities of various tissues and in studying the behavior and properties of the inhibitor-producing system.

Inasmuch as it was possible that the methyl parathion was converted to its oxygen analogue, dimethyl *p*-nitrophenyl phosphate, a standard curve for cholinesterase inhibition with known amounts of this material was prepared. This curve which is also plotted in figure 1 evidently has exactly the same slope as the curve from the metabolite of the methyl parathion. It has been used to calculate the amounts of inhibitor formed in the studies to follow.

It seems probable that the conversion of the thionophosphates to anticholinesterases, as demonstrated in Table II and figure 1, is the result of the action of an enzyme system. Therefore, the amount of inhibitor formed should be directly proportional to the time of reaction and the amount of enzyme present, if other conditions such as the pH of the medium, the temperature, and the amount of substrate remain constant. To study the effect of the time of reaction, the foreguts of several American roaches were incubated as previously described with 3.3×10^{-4} M. methyl parathion for intervals of 30, 60, and 120 minutes. The inhibitory values obtained were converted to concentration of inhibitor, using figure 1. When these values are plotted against the time of reaction a fair approximation to a straight line results. Therefore, it is evident that the reaction is of zero order, as long as the substrate concentration is not appreciably reduced. With the assumption that the activation consists in oxidation to the oxygen analogue, dimethyl *p*-nitrophenyl phosphate, a calculation can be made of the actual amount of inhibitor formed. When the per cent inhibitions

shown in Table III are converted to γ of dimethyl *p*-nitrophenyl phosphate it can be shown that the foregut of *P. americana* produces about 1.0 γ of dimethyl *p*-nitrophenyl phosphate per mg. of dry weight per hour under the conditions of the experiment. This is very consistent with the high toxicity of the dimethyl parathion, to this insect, the topical LD_{50} being about 2 γ per gram of body weight.

From the data in Table II, it appears that several types of thionophosphate esters are readily converted to active anticholinesterases by the enzyme action described. These include several aryl alkyl thionophosphates, an aryl alkyl thionophosphonate, and two trialkyl

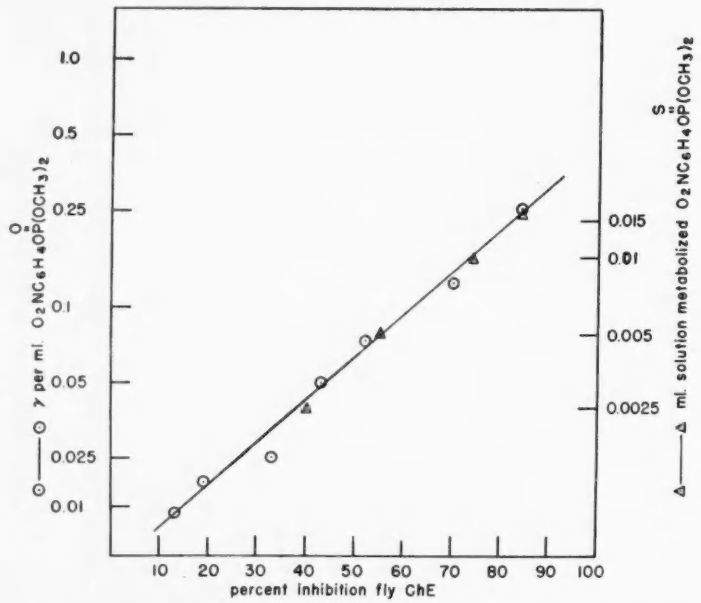

FIG. 1. Curve for relating various percentages of fly brain cholinesterase inhibition, to ml. or micrograms of inhibitor. Left ordinate and points O - - - - O refer to standard curve obtained with known amounts of *p*-nitrophenyl dimethyl phosphate. Right ordinate and points Δ - - - - - Δ obtained with known volumes of supernatant from incubation of *p*-nitrophenyl dimethyl thionophosphate with cockroach gut.

dithiophosphates. Work with additional thionophosphate substrates is complicated by the difficulty in obtaining entirely pure thionophosphates which are not slightly contaminated with S-isomerides. The presence of these latter compounds with their high anticholinesterase activity makes it nearly impossible to study the enzymatic conversion of the thionophosphates to phosphates, with the ChE inhibition technique. However, it seems possible that all the toxic

thionophosphate compounds which are *in vivo* anticholinesterases may be activated in this manner.

Properties of enzyme system which produces inhibitor.—Using the method for incubating methyl parathion with cockroach gut as outlined above, studies were made of the conditions which affected the production of inhibitor. As is shown in Table IV, the reaction is aerobic and does not proceed appreciably in an atmosphere of N_2 and CO_2. Although glucose was routinely used in the tissue incubation studies,

TABLE III

RATE OF PRODUCTION OF ANTICHOLINESTERASE FROM 3.3×10^{-4} M. METHYL PARATHION BY FOREGUT OF *P. americana*

Time Incubation	Per Cent ChE Inhibition Diluted 1:10	Ml. Inhibitor Solution from Figure 1	γ Dimethyl *p*-nitrophenyl Phosphate Formed
30 min	53	0.0045	2.1
60 min	82	0.013	6.6
120 min	90	0.019	9.1

TABLE IV

PRODUCTION OF INHIBITOR FROM 3.3×10^{-4} M DIMETHYL *p*-NITROPHENYL THIONOPHOSPHATE BY COCKROACH GUT UNDER VARYING CONDITIONS

	Condition	Per Cent ChE Inhibition Diluted 1:10	γ Inhibitor Formed Per Flask
A.	Entire gut + O_2 + glucose	99	13
	Entire gut + O_2 (no glucose)	99	13
	Entire gut + 5% CO_2 — 95% N_2 + glucose	30	0.87
B.	Foregut + O_2 + glucose	44	1.5
	Foregut + 5% CO_2 — 95% N_2 + glucose	0	0
C.	Homogenized gut + O_2 + glucose	0	0
D.	Entire gut heated 75° C. — 10 minutes + O_2 + glucose	0	0

its presence did not appreciably effect the amount of inhibitor formed. The reaction was completely prevented by heating the gut to 75° C. for 10 minutes, and by homogenizing the gut tissue. This would seem to indicate that the conversion is enzymatic and requires several enzymes in a system or an enzyme plus coenzyme system. The inhibitor produced was completely stable upon standing for 96 hours in the Krebs-Ringer solution in the refrigerator, as was an equivalent concentration of dimethyl *p*-nitrophenyl phosphate. Under these

conditions 0.1 ml. of inhibitor solution produced 73 per cent ChE inhibition after 24 hours and 76 per cent after 96 hours.

The effects of varying the hydrogen ion concentration of the fluid in which the incubation takes place were studied using the phosphate buffer of Sorenson and the veronal buffer of Michaelis (Gortner and Gortner, 1949). It is evident from figure 2 that the optimum pH

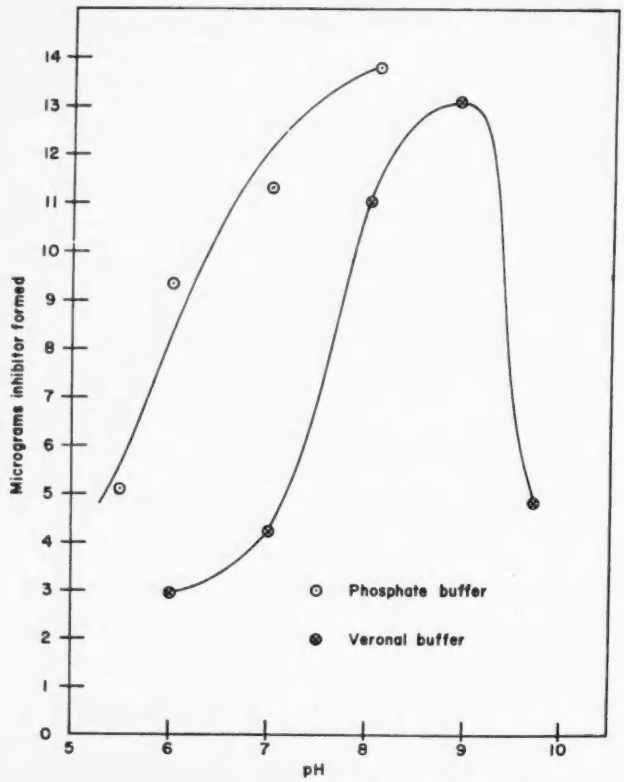

FIG. 2. Effects of variations in pH of buffered medium on amount of cholinesterase inhibitor formed from *p*-nitrophenyl dimethyl thionophosphate by incubation with cockroach gut.

for enzymatic conversion lies between 8 and 9. The amount of inhibitor formed per gut was appreciably greater with the phosphate buffer than with the veronal buffer. This phenomenon has also been observed with urease (Sumner and Somers, 1943).

Effects of enzyme inhibitors on oxidizing system.—The effects of a number of substances known to inhibit various types of enzymes were studied in order to gain some idea of the nature of the system involved

in thionophosphate activation. These inhibitors were added in known concentrations to the modified Ringer solution containing the cockroach gut and allowed to incubate for 1 hour at 37° C. The methyl parathion was then added to make the solution 3.3 x 10^{-4} M., the flasks oxygenated and allowed to incubate for an additional hour. The production of anticholinesterase was then determined as before. The effects of the oxidation-enzyme inhibitors were calculated by determining the amounts of cholinesterase inhibitor produced (from figure 1) and comparing this with a standard containing no oxidation-enzyme inhibitor, the results given in Table V were obtained. They indicate the oxidation system to be poisoned by HCN, hydroxyl amine,

TABLE V

INHIBITION OF THIONOPHOSPHATE OXIDASE BY VARIOUS MATERIALS

Inhibitor	Molar Concentration	Per Cent Inhibition of Anticholinesterase Production
Hydrogen cyanide	10^{-2}	71
	10^{-3}	83
Hydroxyl amine	10^{-3}	100
Malonic acid	10^{-3}	21
Sodium fluoride	10^{-3}	0
Sodium azide	10^{-3}	66
Sodium fluoroacetate	10^{-3}	0 – 14
Iodoacetic acid	10^{-3}	91
Chloropicrin	10^{-3}	100
	10^{-4}	97
	10^{-5}	75
Sodium selenite	10^{-3}	81
Sodium arsenite	10^{-3}	6
Mercuric chloride	10^{-3}	83

iodoacetic acid, sodium azide, sodium selenite, mercuric chloride, and chloropicrin. Chloropicrin was especially effective indicating that a portion of the oxidizing system probably contains an enzyme having active sulfhydryl groups (Mackworth, 1948). The effects of these inhibitors would suggest that a complex oxidase system involving an iron containing enzyme which is inhibited by cyanide and azide (such as cytochrome oxidase) and an enzyme with active sulfhydryl groups inactivated by iodoacetate and chloropicrin (such as succinic dehydrogenase) is responsible for the activation of the thionophosphates.

Efficiency of various tissues in conversion of thionophosphates to inhibitors.—To gain an idea of the tissues of the cockroach which were most active in promoting the enzymatic conversion of the thionophosphates, determinations were made of the amount of anti-

cholinesterase activity produced by incubation of methyl parathion with various organs. Dry weights of these tissues were determined and are used in comparing the relative activities. It should be mentioned that the tissues used undoubtedly vary in activity from animal to animal, hence the values given in Table VI are only approximations. The foregut of the cockroach was most active in the conversion followed by the malpighian tubes, the midgut, nerve cord, and hind-gut, and fat

TABLE VI

EFFICIENCY OF VARIOUS TISSUES FROM *P. americana* IN CONVERTING DIMETHYL *p*-NITROPHENYL THIONOPHOSPHATE TO ANTICHOLINESTERASE

Tissue	Per Cent ChE Inhibition at Dilution		λ Inhibitor per Sample	γ Dry Wt. Tissue mg.	γ Inhibitor per Gram Dry Wt. Approximate
	1:10	1:30			
Entire gut	99		12.4	11.7	
		73	14.0	11.7	1200
Foregut (+ crop)	44		1.5	4.9	3100
	46		1.6		
Midgut	60		2.8		
	69		4.0	8.0	500
Hindgut	38		1.2	7.0	170
	30		0.9		
Malpighian tubules		20	1.7	2.4	730
	75		5.0		
Fat body	49		1.8	12.3	150
Nerve cord		16	1.5	3.7	400
Cuticle		0	0	10.9	0
Muscle		0	0	5.1	0
Mouse liver slice		91	28.5	48.0	590

body. Muscle and cuticle were inactive. Mouse liver, which was the only mammalian tissue investigated, was highly active.

Demonstration of active anticholinesterase by paper chromatography.—Excellent separations of various phosphate and thionophosphate esters have recently been obtained by reversed phase paper chromatography (Metcalf and March, 1952) using Whatman No. 1

paper impregnated with a silicone[4] and the upper phase of a mixture of absolute ethanol—10 parts; chloroform—10 parts and water—6 parts as a solvent. This method was used to demonstrate the presence of metabolites of parathion and methyl parathion in the following experiments.

Warburg flasks containing 3.3 x 10^{-4} M. purified parathion or methyl parathion in Krebs-Ringer solution and a cockroach foregut were oxygenated for 10 minutes and incubated for 3 hours at 38° C. Control flasks without the insect tissue were also run. The contents of each flask was extracted with 2 ml. diethyl ether, the ether solution evaporated to dryness and the residue taken up in 50 microliters of acetone. The acetone solutions were applied as small spots to the silicone-treated paper. After ascending chromatography the papers were developed by spraying with 5 per cent aqueous sodium hydroxide and heating at 105° C. for 15 minutes. Under these conditions the phosphate esters hydrolyzed to give the intensely yellow *p*-nitrophenate ion. The ether extract of the control flasks produced only a single spot $R_F = 0.04$ for parathion, and $R_F = 0.14$ for methyl parathion. However, the ether extract of the flasks containing the cockroach gut produced two spots with parathion, $R_F = 0.04$, and $R_F = 0.70$; and two spots with methyl parathion, $R_F = 0.14$, and $R_F = 0.82$. Within reproducible limits, the R_F values for the two upper spots were identical with control spots of the respective oxygen analogues—para-oxon $R_F = 0.71$, and dimethyl *p*-nitrophenyl phosphate (methyl para-oxon) $R_F = 0.81$, thus providing additional evidence of the enzymatic oxidation of the thionophosphates to the corresponding phosphates. In several of the experiments performed, traces of free *p*-nitrophenol $R_F = 0.78$ were formed by hydrolysis. This was readily distinguished from the intact phosphate esters by the difference in R_F and the fact that the yellow *p*-nitrophenol spot was visible without the sodium hydroxide hydrolysis and heating.

SUMMARY AND CONCLUSIONS

Thionophosphate insecticides such as parathion and its methyl analogue O,O-dimethyl O-*p*-nitrophenyl thionophosphate have been shown to kill insects by inhibition of the cholinesterase enzyme. However, when highly purified, these insecticides do not inhibit insect cholinesterase *in vitro* to any appreciable extent. It has been demonstrated that highly purified thionophosphates are converted to toxic anticholinesterases presumably the oxygen analogues, i.e., diethyl *p*-nitrophenyl thionophosphate to diethyl *p*-nitrophenyl phosphate, by

[4]Dow Corning 550.

an enzyme system present in insects and mammals. This conversion takes place *in vitro* under aerobic conditions in the presence of mouse liver slices or tissue from *Periplaneta americana* (L.). The reaction is prevented by heating or by homogenizing the tissues, and by the presence of cyanide, azide, selenite, iodoacetate, hydroxyl amine, and chloropicrin. In the cockroach the maximum conversion rate takes place between pH 8 and 9, and the highest activity is found in the fore-gut, with lesser activity in malpighian tubules, mid-gut, nerve cord, hind-gut and fat body. Reversed phase paper chromatography of ether extracts of breis of parathion and methyl parathion with cock-roach gut, showed the formation of compounds having R_F values equal to those of the oxygen analogues, para-oxon and methyl para-oxon, respectively. From the results of the experiments discussed, it appears that the *in vivo* conversion of parathion and related thionophosphate insecticides to active anticholinesterases may be responsible for their toxic action to insects and mammals.

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THE ORIENTATION OF DROSOPHILA TO PLANE POLARIZED LIGHT

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The role of polarized light in the orientation of the honey-bee has recently been elucidated by von Frisch (1951). He demonstrated that bees can orient by means of a polarized light compass reaction between the hive and feeding station using only the plane of polarization of sky-light. Vowles (1949) and Schifferer (1950) have demonstrated that the ants *Myrmica ruginodis* and *Lasius niger* can also orient using the plane of polarization of light. Orientation by means of polarized light has thus been demonstrated only for hymenopteran insects.

The frequency of the optic nerve discharge of *Limulus* has been shown by Waterman (1950) to vary systematically with the plane of polarization of the light incident on the eye. Also, Autrum and Stumpf (1950) found that the magnitude of the electroretinograms of the honey-bee and the dipteran, *Calliphora erythrocephala*, was greater when the stimulating light was polarized than when the light was of equal energy, but nonpolarized.

Waterman (1951) has provided a brief review of orientation to polarized light by arthropods and a theoretical discussion of some aspects of the problem of the perception of the plane of polarization of light.

In view of these facts, it seemed pertinent to determine if a non-hymenopteran insect could orient using the plane of polarization of light under optimum conditions and to discuss the characteristics of such an orientation should it occur. Stephens, Fingerman, and Brown (1952) have published a preliminary report of this investigation.

MATERIALS AND METHODS

Black-bodied, vestigial-winged (b vg) *Drosophila melanogaster*[3] were employed in these experiments without regard to sex or age. The following apparatus was designed to permit control of the orientation of the plane of vibration of plane polarized light. A lamp, whose intensity could be varied, was employed and was masked except for a single aperture. Rays passing through this aperture also passed a sheet of ground glass, 16 mm, in diameter, inserted to ensure as even illumination of the orientation field as was possible with this light source, and a piece of plane polarizing plastic. The ground glass and plastic were attached to a sleeve which could be rotated, permitting the plane of polarization to be positioned at will without disturbing the light source.

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This light source was positioned approximately 50 cm. above a horizontal table top which served as the orienting plane. A sheet of polar coordinate graph paper was centered beneath the source to facilitate estimation of the angle of the path followed by the organism.

In conducting a series of trials, the following procedure was adopted. The flies to be used were placed in the darkroom at least thirty minutes in advance of use so that they were dark-adapted. They were kept in darkness during the progress of a set of readings except when it was necessary to remove the animal actually to be used. After the intensity of the polarizing light source had been adjusted with all extraneous light excluded, one of us (G. S.) assumed a position at 0° in terms of the field of orientation, and another (M. F.) took a position at 270°. Readings were taken by dropping a fly at the center of the polar coordinate paper. The direction in which the animal was traveling at the moment of crossing a circle, 5.7 cm. radius, inscribed on the paper was recorded. Readings were taken by G. S. and recorded by M. F. No attempt was made to shield the surface on which the animals were orienting to prevent their being influenced by movements of the observers. The only control used to eliminate such variables lies in the use of two positions of the polarization plane. It was felt that any differential response which was being influenced by the plane of polarization could be distinguished by a comparison of the curves obtained for the two polaroid positions.

Twenty, or in some cases forty, readings were taken with each animal. The polaroid was positioned so that light passing through was vibrating at 175° in terms of the orientation field, ten trials taken, the position changed so that the plane of vibration was at 85°, and ten more trials taken. In the first experiments performed at an intensity of 0.4 foot-candle, the order of positioning of the polaroid was designedly varied and it was determined that this order did not influence the results obtained.

The intensities of 10.0 foot-candles and 0.4 foot-candle were obtained simply by adjusting the current flowing through the lamp and measured with a Weston photometer. The intensity of 0.01 foot-candle was obtained by using a translucent, white-paper filter between lamp and ground glass and was calculated on the basis of the percentage of light transmitted by the filter at a higher intensity.

An additional variable which was not controlled was possible surface variations in the paper on which the flies oriented. It was felt that this variable could similarly be eliminated by the use of two positions of the polaroid filter.

The path traveled by the animal was estimated to the nearest ten degrees by reference to the radiating lines, at each ten degrees, printed on the polar graph paper. The only precaution taken to avoid subjective factors in taking the data was an attempt on the part of the reader to avoid consciousness of the position of the polaroid. Reading was further controlled in that it was under the observation of the recorder who tacitly agreed to estimations.

A control series was done at 1.0 foot-candle by removing the polaroid filter from the light source and taking readings as described above.

RESULTS

1. *Intensity of 0.01 foot-candle.*

The curves of response for the alternate positions of the polaroid (fig. 1, A and B) show no significant difference. There appear to be three clear cut peaks in both curves, at 0°, 90°, 180° but no corresponding peak at 270° in terms of the field of orientation. This lack of a peak at 270° may be a result of the fact that at this very low intensity it was necessary for the recorder to work in close proximity to the orienting surface, possibly disturbing the animals.

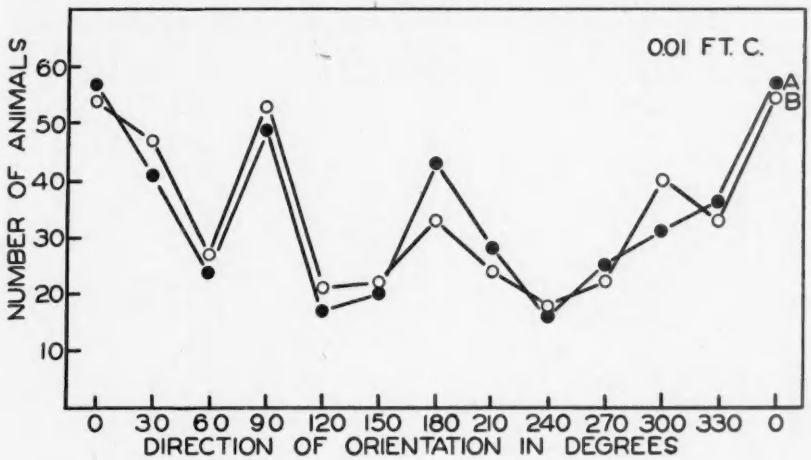

FIG. 1. The direction of orientation of *Drosophila* exposed to normally incident plane polarized light at an intensity of 0.01 foot-candle.
A. Plane of light vibration 175°–355°.
B. Plane of light vibration 85°–265°.

2. *Intensity of 0.4 foot-candle.*

The curve for orientation of animals subjected to normally incident light polarized at 175° (fig. 2, A) shows primary maxima at 0° and 180° with the suggestion of a secondary peak at 270°. On the other hand, when the polaroid was positioned to allow the light to vibrate at 85° (fig. 2, B), the primary maxima observed are at 90° and 270° with a possible secondary peak at 180°. The range of difference in numbers of animals following various paths is as much as three-fold in both cases.

3. *Intensity of 10 foot-candles.*

The same peaks described for the 0.4 foot-candle experiment persist but with considerable increase of the secondary peaks. The curves in both cases (fig. 3, A and B) show less striking differences between the peaks and valleys.

4. *Control at 1.0 foot-candle.*

The control (fig. 4) has a broad maximum at 180° and a minimum at 0°. Since it has been anticipated that the control curve would be

linear, it was assumed that this peak must have been due to extraneous factors. The control was, therefore, repeated with the animals orienting in a black box and the recorder not in the darkroom. The results were essentially indentical with those depicted in figure 4. An asymmetry was then found in the filament of the lamp causing the field to be non-uniformly illuminated.

DISCUSSION

The results of these experiments indicate that *Drosophila* is capable of perceiving and responding to the plane of polarization of plane polarized light under optimum conditions. Under such conditions, they tend to orient in such a fashion that the long axis of their body is parallel to the direction of vibration of the light. This response is most clearly shown at 0.4 foot-candle of the intensities employed in these

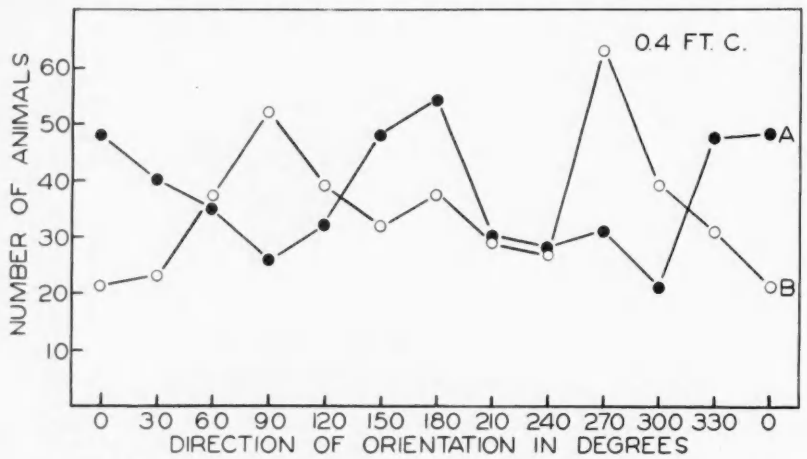

FIG. 2. The direction of orientation of *Drosophila* exposed to normally incident plane polarized light at an intensity of 0.4 foot-candle.
A. Plane of light vibration 175°–355°.
B. Plane of light vibration 85°–265°.

experiments (fig. 2). An examination of this graph, which represents the number of animals orienting in the directions indicated along the abscissa, indicates that the primary maxima for both positions of the polaroid coincide with the axis of light vibration. This response is still evident, though reduced in sharpness, at 10.0 foot-candles (fig. 3).

The two positions of the polaroid were apparently without significant differential influence on the orientation of the animals at an intensity of 0.01 foot-candle (fig. 1). However, a tendency to assume an orientation either parallel or normal to the direction of vibration of the polarized light persists.

We may tentatively summarize the results of these experiments as follows:

1. *Drosophila* is capable of orienting with respect to the polarization plane of normally incident light at all of the intensities investigated.

However, there is an optimal range of intensities throughout which the animal tends to align the long axis of its body parallel to the direction of light vibration.

2. At low intensities the animals continue to respond to the direction of polarization but do not obviously favor a position parallel to the direction of light vibration over a position normal to it. However, either of these positions is favored over other positions.

3. At higher intensities, an increase in the magnitude of the secondary peaks (normal to the direction of vibration of the light) is observed.

4. With increasing intensity, the maxima and minima observed become less sharp under the conditions of these experiments.

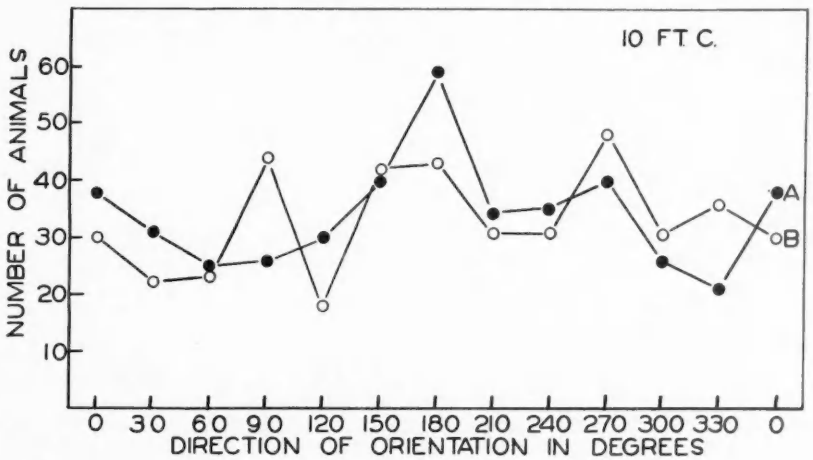

FIG. 3. The direction of orientation of *Drosophila* exposed to normally incident plane polarized light at an intensity of 10.0 foot-candles.
A. Plane of light vibration 175°–355°.
B. Plane of light vibration 85°–265°.

In discussing these results, we are concerned with two problems: possible mechanisms of this orientation reaction, and the significance of the occurrence of an intensity optimum.

A. Possible mechanisms of perception of polarization plane:

Waterman (1951) has recently provided a discussion of this problem in relation to the work on arthropods by von Frisch and other investigators and his own observations on *Limulus*. He states that two things are necessary in an optical system which is capable of polarized light analysis. Such an optical system must 1) be birefringent, and 2) possess some means of eliminating one of the birefringent rays produced.

It seems relevant in the light of the results reported above to suggest an additional set of physical phenomena which could operate to permit polarization analysis by a non-birefringent optical system. The percentage of light refracted at the interface of two non-birefringent

media is a function of the angle of incidence, the indices of refraction of the media, and the plane of polarization. These relationships are expressed in Fresnel's Laws which predict that at all angles of incidence, save 0° and 90°; light vibrating in the plane defined by the incident and reflected rays will be more efficiently refracted than light vibrating in a plane normal to this. The differences in the percentage of the incident light entering the second medium at various angles of incidence are presented in table I which is constructed assuming passage from air to a homogeneous medium whose index of refraction is 1.55, approximately that of the insect cornea (Richards, 1951).

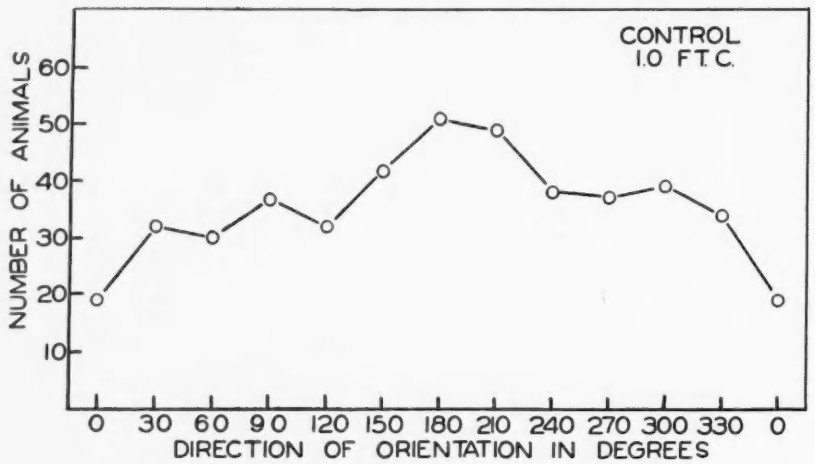

FIG. 4. Control experiment showing the direction of the path followed by *Drosophila* exposed to normally incident nonpolarized light at an intensity of 1.0 foot-candle.

The following facts seem to offer support for the possibility of operation of such a mechanism of polarization analysis in *Drosophila*.

1. There is no evidence of any light compass reaction in *Drosophila* and there is no reason to think that this capacity to distinguish plane of polarization is normally functional.

2. Brief experiments were conducted using the standard two-light technique to verify the fact that our strain of *Drosophila* respond positively telotactically. This reaction is the result of equalization of light from one of the sources on the frontal ommatidia and involves some mechanism for rendering the other source ineffective in producing orientation. When normally incident polarized light is used as a stimulus that portion of the light refracted by those ommatidia directed anteriorly would be maximal when the animal's long axis was parallel to the direction of light vibration. This might explain the preference for this position manifested under optimal conditions.

B. Significance of the intensity optimum:

Hecht and Wald (1934) have demonstrated that the capacity of

Drosophila to discriminate intensities falls off markedly at low intensities. This could account for the increase of the secondary peaks in the orientation at 0.01 foot-candle. Thus the animals would continue to equalize the stimulation of the anterior ommatidia. However, the perceived difference between maximum and minimum stimulation (orientation parallel to or normal to the plane of vibration of the light) would decrease at low intensities. This would explain the increase in magnitude of the secondary peaks at low intensities and their persistence even at optimal intensities, since at all intensities orientation normal to the plane of vibration would produce equal stimulation of the frontal ommatidia.

It is difficult to frame a corresponding explanation by referring to individual ommatidia or to the whole eye as a birefringent polarization analyzer. Such a viewpoint also makes it difficult to explain the occurrence of secondary peaks in the response curves. However, such

TABLE I

REFRACTION OF LIGHT PASSING FROM AIR INTO AN HOMOGENEOUS MEDIUM OF REFRACTIVE INDEX 1.55

Angle of incidence	Component of light vibrating parallel to refractive surface (% refracted)	Component of light vibarting normal to refractive surface (% refracted)
0	95.35	95.35
10	95.16	95.53
20	94.55	96.08
30	93.36	97.00
40	91.23	98.25
50	87.46	99.54
60	80.65	99.88
70	68.01	96.00
80	44.26	76.66
90	0.00	0.00

secondary peaks become a predictable concomitant of the response if the mechanism mediating it is, in fact, dependent on the shape of the corneal-air interface. This is the case since the explanation suggested here involves the operation of the normally operating telotaxis of *Drosophila*.

Two possibilities may be suggested to explain the decrease in the sharpness of the peaks with increase in intensity of the light above an optimum. Carpenter (1905) has demonstrated that *Drosophila* shows a kinesis. It is possible that this might operate to mask partially the telotactic orientation. It is also possible that the decrease in sharpness of response may be the result of a greater influence of extraneous reflected light from the investigators and equipment.

The operation of the mechanism postulated above involves perception of light which does not impinge parallel to the long axis of the ommatidium being stimulated by it. The following information supports this possibility.

1. Vowles (1949) used normally incident plane polarized light in assaying the reactions of the ant, ***Myrmica***. This animal proved to be capable of polarization analysis although worker ants apparently have neither ommatidia nor ocelli directed dorsally.

2. Essentially similar experiments conducted in this laboratory with a locally collected ant (tentatively identified as *Aphaenogaster* sp.) indicate that this animal is also capable of responding to the plane of polarization of normally incident light. Here also apparently neither ommatidia nor ocelli are directed dorsally in the workers.

3. Fingerman (1952) has demonstrated that the ommatidia of the compound eye of ***Drosophila*** can be stimulated by light impinging upon the ommatidia obliquely.

In summary, the mechanism postulated above gains support (a) from the occurrence of secondary peaks and an intensity optimum in the response of ***Drosophila***, (b) from the fact that this capacity for polarization analysis is not normally functional, and (c) this mechanism does not involve postulation of any additional sensory or central nervous capacities beyond those known normally to be operative.

The responses of the honey-bee seem to be too complex to be readily explained by such a simple mechanism of polarization analysis. However, in view of the possibility of explaining the perception of plane of polarization as a function of the shape of the corneal-air interface, it may be suggested that considerable caution is required in drawing conclusions from work which is not supplemented by ethological evidence of a normal role of polarization plane in stimulation of the animal involved. The possibility that responses to polarized light may be explained on the basis of an apparent differential brightness in the visual field as a result of differential refraction of light with respect to its polarization plane, must be experimentally eliminated before a birefringent mechanism of analysis need be assumed.

SUMMARY

1. ***Drosophila melanogaster*** can perceive and respond to the plane of polarization of normally incident plane polarized light under suitable conditions.

2. At light intensities within an optimal range, the animal tends to orient by aligning the long axis of its body parallel to the direction of vibration of the polarized light.

3. At low intensities, the animal shows no marked preference for a position parallel to the direction of light vibration over a position normal to this direction. However, either of these positions is preferred to intermediate positions.

4. Possible mechanisms mediating this response are discussed.

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FLEAS, FLUKES AND CUCKOOS, by MIRIAM ROTHSCHILD AND THERESA CLAY. Pp. xiv+304, 40 plates. New Naturalist Series, Philosophical Library, New York. Price $8.75.

This interesting work concerning the relationships that exist between birds and their parasites is written by two outstanding British zoologists. Miss Rothschild has written many papers dealing with parasites of birds, particularly bird-fleas. Miss Clay is an authority on bird-lice and has published many papers on this subject.

The work has chapters headed Parasitism, Commensalism, Symbiosis, Effect of Parasites on the Host, Effect of Parasitism on the Parasite, Origins of Parasitism and the Evolution of Parasites, Fleas, Feather Lice, Protozoa, Worms, Flies, Mites, Micro-Parasites, Fauna of Bird's Nests, Skuas and the European Cuckoo. The photographs are excellent and the structures of fleas and lice are shown in detail with beautiful micro-photographs.

The reader's attention is drawn by the emphasis placed upon parasitism as a wide spread biological relationship developed through evolution. The advantages and the handicaps of a parasitic livelihood are pointed out very nicely with examples to illustrate each point. The modifications of the parasite to meet the needs of its dependent existence are pointed out in a unique manner, for example, "Birds with the 'gapes' are racked by coughing—a sort of recurrent earthquake for the worms in their throats—and it is, therefore, scarcely surprising that these nematodes live with their anterior ends embedded in the mucous membrane of the birds' tracheae." The reader is reminded that many animals do not carry on basic functions in the same manner as does man and these differences are normal for the animal involved. To summarize this idea the authors state, "It is difficult for them (humans) to realize that fleas breathe through holes in their sides, have a nerve cord below their stomachs and a heart in their backs; or that certain other arthropods lay eggs through their elbows, urinate through their heads and regularly practice virgin birth."

Perhaps the most important contribution of the work is the idea that a better understanding of the relationships between groups of birds can be made as the result of a comparative study of bird parasites. The ostrich and the rhea are now placed in separate orders yet both are parasitized by a genus of feather louse (*Struthiolopeurus*) that is not found on any other birds. Both birds are parasitized by closely related subspecies of the same tapeworm (*Houttuynia struthiocameli*) which is not found in other birds, also two species of mites parasitize both hosts. The occurrence of these common parasites of the ostrich and the rhea cannot be explained by the current theories concerning the origin of the two hosts.

Fleas, Flukes and Cuckoos is an absorbing book to read and it presents many new ideas to both the biologist and the lay reader. In addition it very neatly summarizes some of the concepts that biologists have for a long time stated rather vaguely. Both the authors and the editors are to be congratulated for the production of this work—C. W. MCNEIL

APHELINID BIOLOGIES WITH IMPLICATIONS FOR TAXONOMY[1]

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When a biologist ventures to discuss the taxonomic implications of insect behavior, his reasons for doing so are necessarily extraordinary. In the present instance the first reason, of course, is the invitation to present to you the biologies of the Hymenoptera in which I am most specially interested, relating the discussion of biology to taxonomy insofar as this is practicable. Secondly, and basic in my case, is the frustration exhibited by a colleague of mine, a specialist in the taxonomy of the Aphelinidae, when, confronted with populations of certain aphelinids, he attempts their classification. Although admitting that such populations have the appearance of distinct entities and behave as different species, he still cannot segregate the morphological characters that distinguish them. Thus I know from experience that when the morphologist is at a loss, the biologist must step in and fill in the blanks. If the following discussion is something more than such filling in, then let my frustrated colleague bear the blame.

The identification of certain insects involves the use of behavioral characters. The necessity for thus utilizing behavior occurs when morphological characters are weak or lacking, or when they exhibit intergradations. Since the employment of behaviorial characters is relatively inconvenient, and is usually expensive in time and money, such work is likely to be limited to economic species. Although the differential behavior of organisms, and not differential morphology, is the reason for the existence of taxonomy, its utilization in the identification of species is almost always supplemental to that of morphology.

The use of behavioral characters attains maximum value when the environmental conditions affecting the organisms assessed are similar. The more closely related the organisms, the greater should be the similarity of their environments, so that behavioral differentiation is at its maximum value.

A noteworthy example is in the identification of the closely related citrus scales *Aonidiella aurantii* (Mask.) and *A. citrina* (Coq.). The controversy between the museum taxonomist and the field entomologist concerning the specificity of these scales raged for more than fifty years. Distinct differences in habitat and in parasitic fauna were long apparent to the observer in the field. The museum taxonomist, however, was unable to recognize clear-cut differences in color or structure until McKenzie (1937) studied specimens cultured on citron

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melon (*Citrullus* sp.) under conditions in which color differences were unquestionable.

Another example is found in the genus *Trichogramma*, parasitic on eggs of Lepidoptera. Two common species in North America, *T. minuta* Riley and *T. pretiosa* Riley, not separable morphologically, do not interbreed and differ in their life cycles and habitat preferences. Intergrading color differences occur in the field, but in the laboratory, in a constant environment, color is an excellent taxonomic character (Flanders, 1931, 1938).

During the past twenty years this writer has worked with numerous species of parasitic Hymenoptera and predatory Coccinellidae under fairly constant laboratory conditions. These insects, consisting for the most part of foreign introductions, had to be studied biologically in order to determine their suitability for colonization. One of the most interesting groups of the insects studied is the hymenopterous family Aphelinidae, many species of which play an important role in the biological control of aphids, coccids, and aleyrodids.

Forty-five of the approximately 500 known aphelinid species were studied in more or less detail in the laboratory. These were as follows:

Ablerus sp., a secondary parasite of coccids.
Aneristus ceroplastae Howard.
Aneristus pallidiceps Compere.
Aphelinus mali (Hald.).
Aphytis chrysomphali (Mercet).
Aphytis sp. "A," a primary parasite of *Aonidiella* and *Chrysomphalus* from South China.
Aphytis sp. "B," a primary parasite of *Aonidiella aurantii* (Mask.) from Formosa.
Archenomus sp., a primary parasite of *Lepidosaphes ulmi* L. from France.
Aspidiotiphagus citrinus (Craw).
Aspidiotiphagus lounsburyi (Berlese and Paoli).
Casca chinensis Howard.
Casca sp. "B," primary parasite of *Chrysomphalus ficus* Ashmead from Formosa.
Casca sp. "C," primary parasite of *Aonidiella aurantii* from West China.
Casca sp. "D," primary parasite of *Chrysomphalus dictyospermi* (Morgan) from South China.
Coccophagoides abnormicornis (Girault).
Coccophagoides sp., primary parasite of *Aspidiotus perniciosus* Comstock from North China.
Coccophagus basalis Compere.
Coccophagus capensis Compere.
Coccophagus caridei (Bréthes).
Coccophagus cowperi Girault.
Coccophagus gurneyi Compere.
Coccophagus hawaiiensis Timberlake.
Coccophagus insidiator (Dalman).
Coccophagus ishiii Compere.
Coccophagus japonicus Compere.
Coccophagus lycimnia (Walker).
Coccophagus ochraceus Howard.
Coccophagus pulvinariae Compere.
Coccophagus rusti Compere.
Coccophagus scutatus Howard.
Coccophagus scutellaris (Dalman).
Coccophagus sp., a primary parasite of mealybugs from Hong Kong.
Coccophagus trifasciatus Compere.
Coccophagus yoshidae Nakayama.
Marietta sp., secondary parasite of coccids.
Physcus sp. "B," primary parasite of *Lepidosaphes beckii* (Newman) from Formosa.

Physcus sp. "C," primary parasite of *Pseudaonidia duplex* (Ckll.) from China.
Physcus sp. "D," primary parasite of *Aonidiella* spp. from Pakistan.
Physcus testaceus Masi.
Prospaltella aurantii (Howard).
Prospaltella elongata Dozier.
Prospaltella perniciosi Tower, species feeding on San Jose scale.
Prospaltella perniciosi Tower, species feeding on California red scale.
Prospaltella sp. "B," primary parasite of *Chrysomphalus dictyospermi* from South China.
Prospaltella sp. "C," primary parasite of *Aonidiella aurantii* in laboratory, from Formosa.

Introductions of aphelinids that have been notably beneficial in other parts of the world are *Aphelinus mali* (Hald.), parasitic on the woolly apple aphid; *Prospaltella smithi* Silvestri, parasitic on the spiny blackfly; *Encarsia formosa* Gahan, parasitic on the greenhouse whitefly; *Prospaltella berlesei* (Howard), parasitic on the mulberry scale; and *Eretmocerus serius* Silvestri, parasitic on citrus blackfly (Clausen, 1940).

The accumulation of information on aphelinid biologies has now reached a point where it may be exploited taxonomically. The purpose of the present paper is to describe briefly some of the biological phenomena characterizing certain genera and species of the Aphelinidae, to point out taxonomic values inherent in such phenomena, and to illustrate their use.

FAMILY CHARACTERISTICS

Parasitization by aphelinids is limited to small host insects having sessile stages that inhabit the surface tissues of plants. Aphids and mealybugs when their mouth parts are embedded in plant tissues are sessile from the standpoint of parasite attack.

Superficially, the aphelinid life cycle is simple. No species are known in which the phenomena of polyembryony, alternation of generations, or diapause occur. Observations by various workers over a period of more than fifty years have revealed little out of the ordinary, except that in collections of field material females appear in infinitely greater abundance than males (Howard, 1907).

The developmental period of the individual aphelinid is relatively short, being between 15 and 30 days at temperatures of about 80° F. At these temperatures the maximum longevity of the adult female is about 30 days. It is possible, however, that development may be prolonged by unfavorable nutritional conditions or by low humidities. The number of aphelinid generations per year or per generation of the host (voltinism) is determined largely, if not entirely, by environmental temperatures and by the availability of suitable stages of the host species.

In its general appearance the aphelinid is a minute replica of the honey bee, the adult ranging in length from less than 0.5 mm, as with *Aspidiotiphagus lounsburyi*, to about 2.5 mm, as with *Coccophagus ishiii*.

The significant morphological characters of the family, according to P. H. Timberlake (in unpublished notes), are as follows: Front wings with normal chalcidoid venation; each front basitarsus more or less modified to form a strigil; axillae widely separated, usually distinct but often fused posteriorly with the scutellum and frequently produced

forward into the basal region of the mesoscutum; spur of middle tibia without spines on inner margin. Mesopleura somewhat depressed. Antennae rarely with more than eight segments.

GENERIC CHARACTERISTICS

The taxonomic value of the behavioral characters of the aphelinid genera are unusually high, since the degree of intergradation is comparatively low. As pointed out by Compere (1931), the structural characters used for the separation of many genera, particularly those allied to the genus *Coccophagus*, are relative and cannot be sharply defined.

As our knowledge of aphelinid biologies increases, it becomes more and more evident that biological characters are essential to the final classification of any species. By supplementing behavioral with structural characters when the former are inadequate or unknown, a composite key to the genera is readily set up as follows.

COMPOSITE KEY TO GENERA OF THE APHELINIDAE

1. Females either parasitic or hyperparasitic on nonhomopterous insects 2
   Females primary parasites of homopterous insects 5
2. Females primary parasites (parasitic on species not inhabiting homopterous insects) 3
   Females secondary parasites (hyperparasitic on species inhabiting homopterous insects) 4
3. Antennal scape not greatly expanded . . . . **Centrodora** Först.
   Antennal scape greatly expanded, leaflike . . . . **Tumidiscapus** Gir.
4. Antennae 7-jointed . . . . **Ablerus** How.
   Antennae 6-jointed . . . . **Marietta** Mots.
5. Sex differentiation in host relations absent, reproduction either biparental or uniparental 7
   Sex differentiation in host relation present 6
6. Reproduction either bi- or uniparental 10
   Reproduction biparental only 11
7. Endoparasitic 8
   Ectoparasitic 9
8. Aphidid hosts . . . . **Aphelinus** Dal.
   Diaspid hosts . . . . **Aspidiotiphagus** How.
9. Diaspid hosts . . . . **Aphytis** How.
   Aleyrodid hosts . . . . **Eretmocerus** Hald.
10. Diaspid hosts . . . . **Prospaltella** Ash.
    Aleyrodid hosts . . . . **Encarsia** Först.
11. Females develop only in diaspid scales 12
    Females develop only in lecanine scales and mealybugs 15
12. Female solitary in development 13
    Female gregarious in development . . . . **Casca** How.
13. Oviposit usually in third stage hosts . . . . **Physcus** How.
    Oviposit usually in second stage hosts 14
14. Tarsi 4-jointed . . . . **Archenomus** How.
    Tarsi 5-jointed . . . . **Coccophagoides** Gir.
15. Antennae 8-jointed (classification of species based on coloration) 16
    Antennae 9-jointed, funicle 4-jointed . . . . **Euxanthellus** Silvestri
16. Scape usually fusiformly subcylindrical, not strongly expanded, nor strongly compressed 17
    Scape strongly compressed and expanded . . . . **Prococcophagus** Silvestri
17. Flagellum not compressed; funicle joints usually plainly longer than wide . . . . **Coccophagus** Westwood
    Flagellum compressed; funicle joints about as wide as long or wider than long . . . . **Aneristus** How.

All the known endoparasitic species having homopterous hosts except those in the genus *Casca* and a few species of *Coccophagus* are solitary in their development; that is, only a single individual completes its development in a host individual. Gregarious development commonly occurs in ectoparasitic species such as those of the genus *Aphytis*.

The role of the host in the taxonomy of the parasite is exemplified in the separation of *Aphytis* from the genus *Aphelinus*. Howard (1908b) suggested that it was desirable to segregate the aphid-feeding form from the scale feeders. After Kurdumoff showed that the genotype *Aphelinus abdominalis* Dalman is an aphid-feeding species, Timberlake (1924) adopted Howard's genus *Aphytis* for the coccid-feeding group. Structural differences in the egg-deposition mechanism of these genera are correlated with the type of host.

The primary and secondary parasitism of the aphelinid genera appear to be good taxonomic characters. Forty years ago, Howard (1911), on the basis of numerous observations, stated that the genus *Coccophagus* consisted of species that were primary parasites. His convictions in this respect were, for a time, somewhat shaken by the results of laboratory studies by W. F. Fiske and W. D. Hunter, for Howard remarks that he had to be more guarded in his statements concerning the primary habits of *Coccophagus*.

An additional behavioral character (not utilized in the composite generic key) is the means by which the adult female obtains protein for the completion of oogenesis. The females of *Aphelinus* and *Aphytis* may feed on the body fluids of hosts in order to ripen their full complement of eggs. This nutritional need is not apparent in females of *Coccophagus*, *Prospaltella*, and *Aspidiotiphagus*. *Aphelinus*, using the ovipositor, punctures the body wall of an aphid host and feeds on the fluids that ooze from it (McConnell, 1916; McLeod, 1937). *Aphytis*, likewise, punctures the body wall of its diaspid host, but prior to feeding must construct a waxy pipette from the scale cover to the scale body beneath (C. A. Fleschner, in unpublished notes).

SPECIES CHARACTERISTICS

Since insect speciation is essentially the separation of populations on the basis of behavior, the occurrence of good behavioral characters such as those involving regulation of sex ratio is not surprising. The normal aphelinid male as in other Hymenoptera is haploid in origin, always being derived from an unfertilized egg. With certain aphelinids the male always develops in hosts other than those of the female (Flanders, 1936, 1937, 1946). The sex ratio is consequently regulated in a number of different ways: (1) by the rate of oviposition, as modified by host density (*Coccophagus ochraceus*); (2) by the ratio of male-producing hosts to female-producing hosts, as modified by the length of the pre-mating period of the parasite (many species of *Coccophagus* and *Physcus*); (3) by the proportion of parasitized hosts secondarily superparasitized by the male (*Coccophagus gurneyi* and *C. trifasciatus*); or (4) by the inherent lack of haploid eggs (*Aspidiotiphagus citrinus* and *Aphytis chrysomphali*).

Coccophagus ochraceus will produce all female progeny if artificially prevented from depositing male eggs. This is readily done since the

oviposition posture of the female is sex-related; that is, when about to deposit a female egg, the female takes a stance quite different from that taken when about to deposit a male egg.

Coccophagus scutellaris will produce all female progeny if egg deposition is prevented prior to mating. This results from the fact that all her eggs after mating are deposited under conditions that are lethal to the male, as with certain species of *Casca* and *Physcus*. With *Coccophagus scutellaris*, the sexes are so highly responsive to the mating stimuli that the most competent observers have considered the species to be entirely thelyotokous.

In 1949 and 1950 thousands of females of *Casca chinensis* emerged in the laboratory from California red scales collected in China. No reproduction occurred on red scale, however, until the receipt of two or three mated female parasites that had been collected in China on the foliage of citrus trees. These females oviposited readily in California red scale, but their progeny were all female. Continuous laboratory culture of the species has been impossible, because the source of males is unknown. The converse of this phenomenon occurs with a species of *Prospaltella*, the males of which were reared from red scale parasitized by *Casca*, the host of the female being unknown.

The sex ratio of *Coccophagus gurneyi* is likely to be predominantly male, since the eggs, regardless of sex, are deposited under identical conditions and the male larva invariably destroys the female larva.

The progeny of many aphelinid species, especially in those genera (*Aphelinus* and *Aphytis*) that do not include species having hyperparasitic males, are all female. In such species the female lacks the capacity to deposit haploid eggs.

Although the specific host relations of the female furnish important taxonomic characters, those of the male may not. In certain species of the genus *Prospaltella*, the females invariably develop as primary parasites of certain diaspine scale insects, whereas the males develop as secondary parasites of aleyrodids, mealybugs, or lepidopterous eggs, as well as of diaspine scale insects.

Specificity of parasitization has considerable taxonomic value under both artificial and natural conditions. This value of course varies with the host specificity as represented by the numerical status of the host-list of the parasite species. The fact that a certain parasite species that inhabits different geographical and floral areas may have a host-list for each area differing in the number and kind of hosts does not lessen its value as a taxonomic character. As pointed out by Ashmead (Howard, 1901), a parasitic species, when introduced into a new area, may attack different host species. It is known, also, that many insects which are nutritionally suitable as hosts of a parasitic species never serve as hosts under natural conditions.

The host specificity of a parasite species is the end result of a parasitic reaction chain or sequence of responses of the parasites to environmental contacts (Salt, 1938), each response possibly being a specific taxonomic character. This reaction chain is a selective process involving host-habitat finding, host recognition, and host suitability. Regional differences in host-lists of a species when the suitable hosts in each region are equal in kind is the effect of different environments on the operation of the selection process.

The utilization of the aphelinid parasites of one species of insect to control another is not likely to be realized. Howard (1908a) states that in Florida the control of the citrus whitefly, ***Dialeurodes citri*** (Ashm.), was attempted by introducing parasites of related coccids, without results. Although the citrus whitefly has been in southern United States for more than fifty years, it has acquired no native parasites.

The importance of the host as a taxonomic character is exemplified by the genus ***Euxanthellus*** Silvestri, which appears to be entirely African in origin. It is closely related to the ***Coccophagus*** and is similar in its habits and host relations. Unlike ***Coccophagus***, it lacks good color characteristics for distinguishing its species. Speciation, however, is indicated by combinations of certain minor structural characteristics which are more or less correlated with certain hosts. Compere (1936) distinguishes the following.

Host Key to Nine Species of Euxanthellus

E. subochraceus (How.).....ex *Lecanium* sp.
E. philippiae Silv.....ex *Philippia chrysophyllae* and *Saissetia cuneiformis*
Euxanthellus sp., Ser. 1.....ex *Inglisia elytropappi*
Euxanthellus sp., Ser. 2.....ex *Saissetia perseae*
Euxanthellus sp., Ser. 3.....ex *Coccus hesperidum*
Euxanthellus sp., Ser. 4.....ex *Saissetia oleae*
Euxanthellus sp., Ser. 5.....ex *Ceroplastes destructor*
Euxanthellus sp., Ser. 6.....ex *Eriococcus* sp.
Euxanthellus sp., Ser. 7.....ex *Saissetia hemisphaerica*

Host suitability in a controlled environment is of course a good taxonomic character. When ***Coccophagus gurneyi*** is confined with a mealybug population consisting of two species, it may oviposit readily in both species, although only one of them is suitable for the development of its offspring (Bess, 1939).

Host recognition may also be a character. A species of ***Coccophagus*** from Hong Kong was found to reproduce on ***Pseudococcus citri***, but its eggs were deposited in this mealybug only when the latter was part of a mixed population with either ***P. longispinus*** or ***P. maritimus*** or both. In pure cultures of each of these mealybugs the ***Coccophagus*** recognizes none as a site for the deposition of its eggs.

The effect of environmental factors on the host-list of aphelinid species has often been observed in California. ***Aphytis proclia*** (Walk.) readily reproduces on purple scale, ***Lepidosaphes beckii*** (Newm.), in the laboratory, but not in the field. ***Coccophagus lycimnia*** is the dominant parasite of black scale, ***Saissetia oleae***, on ***Baccharis*** in the vicinity of Santa Cruz in northern California. In the vicinity of Riverside black scale is not a host. All attempts to propagate this parasite on black-scale-infested potato sprouts in the laboratory have failed.

Coccophagus cowperi and ***C. pulvinariae*** are readily propagated on black-scale-infested potato sprouts in the laboratory, but neither species parasitizes black scale in the field. These two species of ***Coccophagus***, according to Compere (1931), belong to the "lecanii" complex of species which also includes ***C. lycimnia***, ***C. japonicus***, ***C. hawaiiensis***, ***C. tibialis*** Comp. and ***C. isipingoensis*** Comp. The species of this group do not appear to be separable by any structural characters.

Recognition of their speciation by Compere (1931), although based primarily on the coloration of the legs, was uncertain until subsequently confirmed by the biological studies of the writer.

Morphologically, the Japanese species *Coccophagus japonicus* and *C. hawaiiensis* intergrade. Differences in natural hosts, in host melanization, and in length of life cycles, and the absence of sex attraction and of sperm transmission, effectively isolate them taxonomically. Competent taxonomic authorities are not in agreement on the status of these species, however. Timberlake (1924) considered them distinct, Gahan thought that they represented a single species, and Compere, undecided, states that it is not unlikely that they are specifically alike (Compere, 1931).

Species separated geographically tend to have some minor structural differences. On the one hand, *Coccophagus lycimnia*, a North American form, and *C. pulvinariae*, an African form, exhibit differences in the number of sensoria on the flagellum, and in the density of the wing setae. On the other hand, *C. lycimnia* and *C. cowperi*, another African form, are so morphologically similar that they were synonymized by Gahan. They are separable, however, by the color of the hind tibia, by differences in hosts in the field, and by the absence of sex attraction and of sperm transmission.

Another *Coccophagus* group consists of *C. scutellaris* and *C. ishiii*. These species differ in habitus, coloration of the coxae, and in hosts. *C. ishiii* does not parasitize the soft brown scale, *Coccus hesperidum*, although *C. scutellaris* does so. A behavorial key to a few species of the genus *Coccophagus* follows.

COMPOSITE KEY TO TEN SPECIES OF COCCOPHAGUS

(See Compere, 1931)

1. Unfertilized eggs not deposited hyperparasitically (the adult progeny of mated females being of both sexes) 2
   Unfertilized eggs deposited hyperparasitically (all the adult progeny of mated females being female) 4
2. Unfertilized eggs deposited endoparasitically 3
   Unfertilized eggs deposited ectoparasitically ..... **ochraceus** How.
3. Female develops only in *Pseudococcus* ..... **gurneyi** Comp.
   Female develops only in *Saisseti*a ..... **trifasciatus** Comp.[3]
4. Unfertilized eggs deposited ectoparasitically 5
   Unfertilized eggs deposited endoparasitically 7
5. Reproduction readily occurs in *Saissetia oleae* on potato sprouts 6
   Reproduction does not occur readily in *S. oleae* on potato sprouts, ... **lycimnia** (Walk.)
6. Femora yellow ..... **pulvinariae** Comp.
   Femora black (a mixed culture of *C. pulvinariae* and *C. cowperi* on black scale is temporary since the former will replace the latter) .... **cowperi** Gir.
7. Content of host not consumed prior to pupation of parasite 8
   Content of host consumed prior to pupation of parasite 9
8. Gregarious in larval development ..... **scutellaris** Dal.
   Solitary in larval development (female embryo forms a trophic membrane), ... **capensis** Comp.
9. Pupa with dorsal thoracic horn ..... **rusti** Comp.
   Pupa without such a horn ..... **hawaiiensis** Comp.

[3] *C. trifasciatus* differs from other species of the genus in that oogenesis may cease within five days after emergence from its host.

The classification of the genus *Aphytis* awaits the acquisition of additional biological information. Each of the present morphological species in this genus appears likely to be a complex of behavioral species.

In the fall of 1947, a behaviorally distinct form of *Aphytis*, live specimens of which were morphologically indistinguishable from *A. chrysomphali*, was received from China. Unlike *A. chrysomphali*, however, it was biparental and had a much larger laboratory host-list. It was first recognized as a distinct form because of a black mark on the venter of the pupa. Highly refined morphological studies by Compere have revealed, at high magnification, a constant structural difference in the marginal crenulations of the mesoscutum. This character, however, is cryptic and not readily ascertained.

Aphytis proclia occurs in many areas inhabited by California red scale but is not known to be parasitic upon it. In 1951 a unisexual form that reproduces readily under laboratory conditions on California red scale was obtained from Formosa. Further biological studies probably will serve to segregate *A. proclia* into two or more species. Compere informs me that he has recently found that the so-called *A. proclia* is made up of three populations that are separable on the basis of color, these populations parasitizing different host species.

To the experienced observer the habitus or posture of a species is a valuable taxonomic character. Unfortunately, in most instances the habitus of a species, although observable, cannot be adequately described. The habitus of *Aneristus ceroplastae* and related species is quite striking, however, being characterized by the tilted abdomen, held at an angle of about 45° from the horizontal.

The genera *Prospaltella* and *Encarsia* are not distinctly separable morphologically, and yet they are separable on the basis of hosts, *Prospaltella* parasitizing only diaspine scale insects and *Encarsia* parasitizing only aleyrodids. Likewise, the different species of *Prospaltella* and of *Encarsia* are characterized by the specific hosts that they attack. An interesting case is that of *Prospaltella perniciosi*, which appears to be composed of three geographical species (Flanders, 1950), a biparental species in the North Atlantic states and a uniparental species in the South Atlantic states, both of which are parasites of San Jose scale, and a uniparental species in East Asia, which is a parasite of the California red scale. The red-scale-feeding species does not attack the San Jose scale, nor does the San-Jose-scale-feeding species attack the California red scale. Both uniparental species are now established in California and are perfectly isolated although morphologically alike. When the biparental and uniparental Atlantic states species are cultured together in the laboratory the uniparental species becomes dominant and eliminates the biparental species, in spite of the fact that the males of this latter species are hyperparasitic. In species in which host specificity is relatively low, a similar situation may exist. *Aspidiotiphagus citrinus* in California does not attack California red scale, yet in East Asia a species occurs that does so. This East Asian species was released in California in 1948 and subsequently recovered there from California red scale.

DISCUSSION

The physiological and psychological (behavioral) characters usable in the taxonomy of the Aphelinidae include the habitus or posture of the adult and its habitat and food preferences, the environmental condition under which the immature stages exist, and the responses of such stages to certain environmental changes.

Lack of interbreeding also is a basic character that may be either physiological or psychological. Evidence of interbreeding is the production of normal biparental progeny. Mating and impregnation are of no value in determining biparentalism, either between species or within species. It should be noted that bisexuality and unisexuality may be purely phenotypic responses and of no value in taxonomy.

These observations on aphelinid biology serve to emphasize the fact that basically taxonomy is behavioristic, differences in behavior being a primary fact of iife. Historically the classification of animals was based on behavior, animals being classified as either aquatic, terrestrial, or air-borne. The development of physiological and psychological differences between populations is essential to speciation, a phenomenon that ultimately becomes manifested by morphological differentiation, the spoor of organic evolution.

Inevitably, the museum taxonomist in his endeavor to work backward along the organic paths of evolution runs out of structural characters. Then, for final identification, he must of necessity search for characters in the behavior patterns of the organism. It is this pattern that actually delimits a species, which, to paraphrase Mayr (1942), is a population behavioristically isolated from other populations. The high degree of specificity in behavior that characterizes many entomophagous species, particularly the Aphelinidae, is a quality of life that is essential, not only to their employment in the biological control of insect pests, but also in determining their final taxonomic relations. It is evident that in the biologies of the Aphelinidae, as presented herein, are taxonomic characters essential to the classification of the species.

SUMMARY

In the hymenopterous family Aphelinidae, behavioral characters are essential in the identification of a number of genera and species. With intergrading species, the values of morphological characters are measured by behavioral characters. The final classification of species morphologically alike is based entirely on behavior. Composite keys are illustrated, using behavioral as well as morphological characters. Although speciation in insects is primarily behavioral, the taxonomic use of behavior when morphological characters are available is unnecessary and usually impracticable.

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FILTH BREEDING FLIES OF GUAM, by GEORGE E. BOHART AND J. LINSLEY GRESSITT. Pp. vii+152, 14 text figs., 17 plates, 1951. Bul. 204, Bernice P. Bishop Museum, Honolulu, Hawaii.

So great a role in the transmission of human and animal diseases has been played by the blood-sucking insects that studies of these groups have greatly overshadowed, except for the house fly, those of another important group of Diptera, the filth-breeding flies. We are, however, now coming to the realization that flies that breed in carrion, excrement, and other organic filth, and that then come into contact with the food or bodies of man and domestic animals, may aid greatly in the dissemination of disease. The present work is a good example of what can be done, through intensive work in a restricted area on the filth fly fauna. Though the approach is from a taxonomic standpoint this work deals primarily with the biological aspects. Some material is gleaned from the literature but much of it is new and previously unpublished. About a hundred species of flies are treated; eggs, larvae, pupae, and adults alike, are keyed, and in many cases illustrated in whole or part. The authors come to the conclusion that the most important filth breeding flies on Guam are the calliphorid *Chrysomya megacephala* and the bazaar fly, *Musca sorbens;* the house fly, *Musca vicina*, is far less abundant and consequently of less importance.—M. T. J.

THREE NEW SPECIES OF MICROLEPIDOPTERA (OLETHREUTIDAE, GLYPHIPTERYGIDAE AND YPONOMEUTIDAE)

A. E. BROWER
Augusta, Maine

Aphania paludicolana, new species

Head, thorax and abdomen, grayish fuscous, being clothed with mixtures of light and dark scales, becoming whiter laterally and below. Underside of head and palpi white, the outer portion of the second and the third palpal segment brownish fuscous. The thorax appears light gray with a narrow black transverse basal band and a dorsally broken median band and dark tuft. Forewings with basal two thirds fuscous; the outer portion white, with three fairly distinct gray bars before apex and a faint one obliquely across wing, with terminal and basal lines in the fringe; the outer margin of the dark median area straight and transverse to the cell, then offset outward with a dark spot over the angle, and thence irregularly rounded and oblique to the inner margin before the anal angle; irregular whitish areas on costa near base and from middle of base downward and below line of fold; the lines indistinct but on the best marked individuals seen as black patches, most evident below the fold, where five darker patches occur, and a rather conspicuous rectangular black patch at end of cell. Hind wings light fuscous, with paler fringes. Expanse 16–17 mm.

Types.—Holotype: ♂ Southwest Harbor, Maine, June 12, 1937, A. E. Brower (Brower Coll.). *Allotype:* ♀ Same place and collector, June 8, 1937 (To be deposited in Canadian National Coll.). *Paratypes:* Same place and collector, all 1937, 6♂ 1♀ June 5; 1♂ 1♀ June 8; 2♀ June 12. Part of paratypes will be deposited in the Canadian National Coll. and the U. S. National Museum. All were taken by the author in a black spruce-sphagnum bog, and the specific name refers to this habitat. Dr. J. McDunnough and Carl Heinrich both confirmed my suspicion that this is a distinct species.

The male genitalia are similar to *A. capreana* (Heinrich, U. S. N. M. Bul. 132, Pl. 62, f. 375) but the socii are considerably narrower. The female genitalia are most like that of *youngana* (loc. cit. Pl. 45, f. 270) with the scobinate patches on bursa, but without so strongly developed a pouch-like portion of the ductus bursa.

A description of this species would have little meaning unless a comparison is made with the very similar *Aphania capreana* Hbn. and *A. youngana* McD. It is definitely smaller than these species; the second palpal segment is much whiter laterally; the color grayer brown than the brighter brown superficial scales on *capreana* and the blackish *youngana;* the whitish area along costa begins at base, unlike *youngana*, while the whitish shading from base on fold is much more extensive than on *youngana*, and extends as three to five irregular patches below across the fold (these two white areas are absent or poorly developed

on *capreana*); the outer boundary of the dark area is sharply angled in all three species at end of cell, in *youngana* there is no black spot below on outer corner, this is elongate and closely appressed in *capreana* and rounded and more distinct in *paludicolana;* the black rectangular patch at end of cell is shorter and rather blacker than on the other two species; at the lower end the outer margin of the dark median shade meets the inner margin farther from the tornus than on *youngana* and still farther than on *capreana*. My *capreana* all expand 18 m.m. except one, and the *youngana* range from 18–21 m.m. Another important difference is that *paludicolana* flies a month earlier. *A. frigidana* Pack. has been confused with some of the above because of its similar

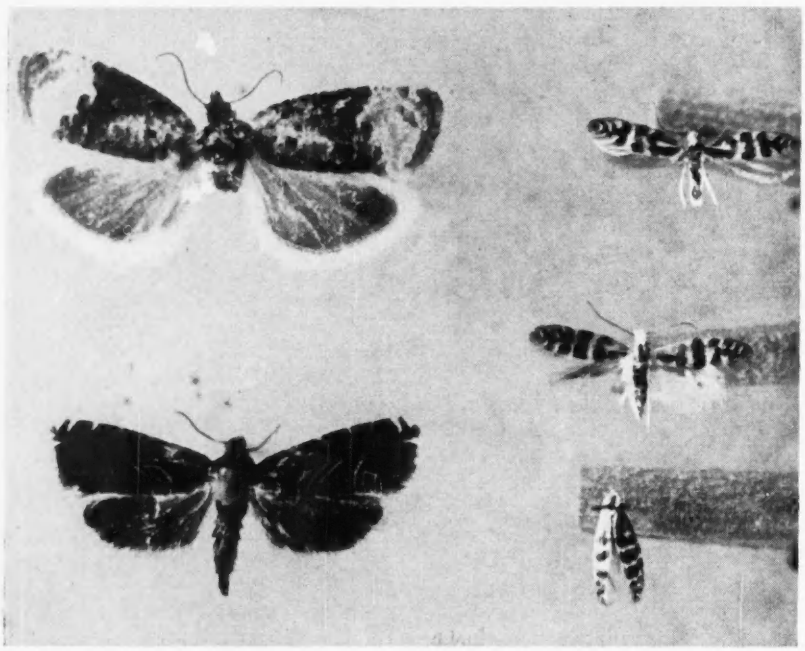


FIG. 1. *Aphania paludicolana* (upper left), allotype female; *Hilarographa jonesi* (lower left), allotype female; and *Argyresthia aureoargentella* (on right), holotype male, allotype female and paratype female (unspread).

general pattern, but the series I collected in the Shickshock Mts. in the Gaspé are readily separable by their narrower wings, much duller darker color and great suppression of the white shades.

Hilarographa jonesi, new species

Head, thorax and abdomen leaden black. The male antennae dark, setaceous beneath; female antennae filiform. Underside of head and palpus white, with second segment fuscous laterally, the third flattened and fuscous anteriorly and with a dark apex. The head surrounded by a fringe of long scales, white except dorsally; lower face white; a

white median line on face, and white lateral lines on face reappearing on neck and on thorax; shoulders creamy white. Undersurface of thorax and legs largely white, the fore and mid-tibiae with two large dark lateral marks, the hind tibiae dark outwardly; all tarsi with two or more dark bands. Abdomen beneath with segments two to seven broadly banded terminally with white, the seventh narrowed and much elongated in the female. Fore wings leaden gray, overlain with and becoming outwardly bright lustrous coppery-red, with some purplish scaling, particularly on the upper half of the wing and between the red bands; a long reddish basal dash and strongly angulate alternating white and red transverse bands, four of each, the white ones becoming faint medially, the two proximal reddish ones becoming whitish near the inner margin, the outer dividing into three fingers near inner margin; toward the apex and outer margin the red bands widen and coalesce in an intricate pattern; wedge-shaped preapical, apical and small subapical white patches; speculum a vertical row of four quadrate black patches, with a small bar above the fourth, and beyond the fourth quadrate patch; beyond these the leaden ground appears. Hind wings fuscous brown; all fringes dark. Expanse male 12 m.m., female 13–14 m.m.

Types.—Holotype: ♂ Martha's Vineyard, Massachusetts, August 6, 1941, F. M. Jones, at light (Brower Coll.). *Allotype:* ♀ Martha's Vineyard, Massachusetts, August 6, 1943, F. M. Jones. (To be deposited in the U. S. National Museum). *Paratypes:* 2 ♀ Same place and collector July 18, 1947 (Coll. F. M. Jones) and August 29, 1946 (Coll. A. E. Brower); 1 ♀ Lakehurst, N. J., July 4, 1909, W. D. Kearfott (returned to U. S. National Museum); and 1 ♀ Orient, Long Island, N. Y., September 2, 1948, Roy Latham (returned to American Museum of Natural History).

This species is named for Dr. F. M. Jones who has taken four specimens of this dashing little moth at Vineyard Haven, Martha's Vineyard, all within one fourth mile. The first at light at the edge of an extensive woodland. The second was seen flying rapidly in a wood road and netted off oak leaves. The third was flying rapidly to and fro for about ten inches between a pitch pine and an oak, about twelve inches above the ground. The fourth was found in the afternoon sitting on the upper surface of an oak leaf, at intervals shifting its position by a twitching lateral movement with readjustment of its wings. This is the first species of *Hilarographa* to be recorded from eastern America. The bright coppery-red ground color of *H. jonesi* distinguishes it from the dark colored *youngella* Busck and *olympica* Braun. *H. regalis* Walsingham has an orange ground greatly reduced by leaden gray and fewer fine markings.

Argyresthia aureoargentella, new species

Head with tuft, face, palpi, eye caps and antennae silvery white, the antennae ringed with dull dark golden or brown. Thorax white with golden shoulders. Legs, underside, and abdomen white or tinged with golden. Fore wings golden with conspicuous silver bars and markings, best developed on the female. Silvery markings as follows: a broad basal dash and less conspicuous light inner margin, separated from

first silver bar by a broad golden band; five silver bars or three bars and two pairs of patches, transversely cross the wing, the first three broadened on the costa and somewhat bowed or angled out in the middle, the first broad and usually appearing definitely angled outward from the costa, the second broad and straighter, the third is narrow and irregular, often broken, the fourth is usually of two inwardly inclined angular marks, the fifth bows inwardly across the tip and is usually complete. There may be an extra costal mark associated with the third bar. A small dark apical spot is present. Fringes light fuscous with golden scaling at apex of forewing. Hindwings pale. Expanse male 7.5–9 mm., female 8–9 mm.

Types.—Holotype: ♂ Rearing lot #49B18, Mariaville, Maine, (north of Ellsworth) emerged 13–VI–49, bred ex *Thuja occidentalis*. *Allotype:* ♀ Rearing lot #49B23, Newport, Maine, emerged 19–VI–49, bred ex *Thuia occidentalis*. Both types will be deposited in the U. S. National Museum. *Paratypes:* 43♂ and 30♀ reared from fifteen collections of *Thuia occidentalis* branches from Mariaville, Guilford, Dexter, Milo, Newport, Millinocket, Island Falls, Reed Plantation, Macwahoc and Indian Town, Maine; and 16♂ 7♀ caught at Chester, Lincoln, Enfield, Etna, Canaan, Newport, Winterport and Bar Harbor, Maine, nearly all collected by the author. Dates of capture range from the end of May until July 18. Paratypes will be deposited in the U. S. National Museum, Canadian National Collection, Cornell University, University of Massachusetts, collection of the author and other collections.

This species is named for its contrasting pattern of gold and silver. The nearest species, *A. freyella*, is somewhat smaller with greatly reduced silvery markings and these duller, becoming lead-colored apically. The prominent transverse silvery bands of *aureoargentella* are replaced by poorly developed bands or outwardly oblique markings arising from the margins. The apical spot is more prominent on *freyella*. *A. freyella* breeds commonly on both *Juniperus virginiana* and on *Thuia*, but the small collections made in Maine of *Juniperus virginiana* and *Chamaecyparis thyoides* have not yielded *aureoargentella;* and probably its somewhat larger size renders feeding in their twigs more difficult. The cocoon of *aureoargentella* is slightly larger and appears whiter than that of *freyella*. Both species form spindle-shaped white silken cocoons on the twigs outside the mines. Packard in his original description of *A. thuiella* confused the larval habits with one of the above, because *thuiella* pupates within the mine with but a silken lining. The moths fly from the end of May into July, being most active on dull or cloudy days and around sundown.

Thanks are due to Dr. J. McDunnough, Canadian National Collection, Carl Heinrich and August Busck, U. S. National Museum for assistance in checking the determination of these three species; and to the Maine Forest Service for permission to include many of the *Argyresthias* in the type series.

A REVISION OF THE GENUS LOXOCERA IN NORTH AMERICA WITH A STUDY OF GEOGRAPHICAL VARIATION IN L. CYLINDRICA

(Diptera, Psilidae)[1]

KENNETH J. CAPELLE

This paper is a systematic revision of the flies of the genus *Loxocera* Meigen from America North of Mexico. The study was based on an accumulation of over three hundred specimens, the members of the genus never being numerous in any one collection.

Emphasis is placed on external morphology of the head, length of antennae and size and shape of the eyes.

The male genital clasper, being extremely minute, is best observed with a compound microscope, after it has been cleared and dissected. The penis is an extremely delicate, membranous organ which is easily destroyed in clearing and especial care must be taken in staining it.

Females, except for *L. microps* are very similar, structurally, to the males and can be determined by the same external morphological characters.

ACKNOWLEDGMENTS

The writer wishes to express his sincere thanks to Mr. C. W. Sabrosky for suggesting the problem, for help, and for the loan of material from his personal collection. The author is further indebted to Dr. C. D. Michener and to Dr. R. H. Beamer for guidance and many helpful suggestions since the beginning of this study.

Appreciation is hereby expressed to the following people and institutions for the loan of material: Dr. C. H. Curran, American Museum of Natural History; Dr. H. H. Ross, Illinois Natural History Survey; Dr. E. S. Ross, California Academy of Science; United States National Museum; Dr. M. T. James, State College of Washington; Mr. J. L. Laffoon, Iowa State College and the Snow Entomological Museum of the University of Kansas.

Mr. Paul Freeman of the British Museum (Natural History) has clarified the question concerning the existence of Walker's type of *Loxocera quadrilinea*.

Especial thanks are due my wife for help in the preparation of this paper.

BIOLOGY AND HABITS

Except for *Psila rosae* Fabricius, the Carrot Rust Fly, very little is known of the life histories of the Psilidae. The majority of the species are suspected to be root burrowers and gall-makers, this being supported by the manner and shape of the female ovipositor which is no doubt fitted for piercing plant tissues. *Chyliza notata* Loew has been reared

[1]Contribution number 786 from the Department of Entomology of the University of Kansas.

from elderberry; *C. leguminicola* Melander has been reared from the legume, *Lupinus polyphyllus*, and *Chyliza* spp. have been reared from rotten wood.

Of *Loxocera*, no host plants are known. The writer has observed numbers of *L. fumipennis* flying about *Digitaria* (crab grass) on a low moist slope late in May, 1951. The males far outnumbered the females, their flight being brief and indefinite. When at rest on the grass, both sexes exhibited a rapid raising and lowering of the abdomen which caused a vibrant fluttering of the wings, very similar in appearance to certain of the sphecoid wasps. Flight was never more than 12 to 18 inches above the ground and partially shaded areas seemed to be preferred to direct sunlight.

On September 11, 1951 the writer observed several *L. fumipennis* and *L. cylindrica* in the same area in which *L. fumipennis* had been observed in May. Males again outnumbered females, and the same rapid fluttering of the wings occurred. Mating was not observed. When at rest on the grass blade, the wings are held parallel over the body and the antennae are porrect, and at right angles to one another.

The interval covered by the two observation dates, April 23 to September 11, would indicate at least two generations occurring during the year, probably more. The male specimen of *L. fumipennis* taken September 11 still had a portion of the ptilinal sac protruding from the lunule region, indicating recent emergence. Both species in the same area were flying about and resting on the sedge *Carex* and crab grass *Digitaria*, though no other associations with these plants were observed.

One female specimen of *L. fumipennis* was collected by the writer at a light June 1, but this is certainly not a common behavior.

Other species have been collected by the author from sweepings on low herbage and grasses in pastures and low meadow lands in the vicinity of streams. The majority of them are early Spring forms and probably short lived. One mating pair of *Loxocera cylindrica* was taken June 23 on Long Island, New York by Dr. C. H. Curran.

Loxocera Meigen

Loxocera Meigen, 1803, Illiger's Mag. für Insektenkunde, 2: 275. Type species: *Loxocera cylindrica* Say, 1823, Jour. Acad. Sci., Philadelphia, 3: 98.

The genus *Loxocera* is probably most closely related to *Pseudopsila* Johnson, but differs from it by the lack of postvertical bristles and a subcylindrical third antennal segment. The third antennal segment is always as long as, or longer than the length of the arista.

Meigen's original description is translated as follows:

"The antennae are forward and angled, three segmented, the first two segments are small, cup-shaped, the third long, line-like, flat with fine bristles at the base. The body is naked. The wings are parallel and blunt."

Probably the most distinctive feature of the genus is the greatly lengthened third antennal segment. This is longest in *L. collaris* where it attains a length almost equal to twice the head height and is shortest in the female of *L. microps* where the entire antenna is but equal to the head height. The third segment is always dark brown to blackish brown and covered with fine pubescence. The arista which is

always shorter than the antenna is also pubescent, the hairs varying somewhat in length and density with the species. Although *L. fumipennis* appears to have a three-segmented arista, other species show but two segments. Antennal segments one and two are short, the first often being concealed by the extension of the front. Sparse, fine bristles are found on both segments, becoming less pronounced in *L. microps* and *L. collaris*. The second segment has a dorsolateral longitudinal seam indicating a relationship with the muscoid Diptera. The face is receding in profile, most strongly so in *L. microps*. The frontal triangle is extended and highly polished, ocellar bristles are present though often weakened, inner and outer verticals are strong. The eyes vary in size, often extending above the front in profile, facets are uniform. The palpi are slender and two segmented. The thorax is elongate, humeri are distinct, the scutellum is bare except for two pairs of scutellar bristles, the anterior pair are considerably weakened. One pair of prescutellar dorsocentrals, two pairs of supra alars, one pair of presuturals are present. Pleural bristles are absent. The thorax varies with the head from deep orange-yellow to pale yellow ocher. Wings are clear to uniformly dusky brown, the subcosta is incomplete, the costa is broken at the end of the subcosta, continuing as a weakening across the basal third of wing. Third and fourth veins are parallel apically except in *L. cylindrica*, the discal cell is always large, second basal and anal cells are approximately equal in size. The wing membrane is uniformly covered with microtrichia. The legs are elongate, yellowish, becoming darker toward the tarsi, apical tibial bristles are present on the second and third legs. A peculiar pad-like ovate spot appears ventrally at the apex of the hind femur. It is found in both male and female specimens of *Loxocera* and *Chyliza*. This was first reported by Collin (1944), who believed it to function as some type of sensory pad. The halteres are pale yellow. The abdomen is elongate, usually darker than the thorax and covered uniformly with fine hairs. The ovipositor is elongate and well developed for piercing. Male genitalia are small and inconspicuous.

KEY TO THE SPECIES

1. Wings uniformly hyaline 2
   Wings uniformly dusky or clouded at apex 4
2. Eye in profile attaining anterior margin of face, length of female antenna longer than head height 3
   Eye in profile never attaining margin of face, length of female antenna equal to head height ..... **microps**
3. Ocellar bristles reaching eye margin laterally, inner verticals convergent and almost touching ..... **collaris**
   Ocellar bristles not reaching eye margin laterally, inner verticles convergent but never touching ..... **californica**
4. Wings uniformly dusky, eye in profile never extending above top of head ..... **fumipennis**
   Wings not uniformly dusky, eye in profile extending above top of head, ... **cylindrica**

Loxocera microps Melander

Plate I, fig. 2; Plate II, fig. 8

Loxocera microps Melander, 1920, Psyche, 27: 92.

The male of this species somewhat resembles *L. collaris* but differs

in that the eye never attains the anterior margin of the face. The female is distinct with its yellow ocher color and short antennae which are never longer than head height. It is readily distinguished from all other members of the genus by these characters.

Male.—Head: Brownish-yellow with black median frontal stripe. Anterior orbits with black ring. Frontal triangle extending to frontal suture and occupying about half of front at ocelli; face strongly receding, antennal grooves covered with fine white hairs, median facial area bare and polished. Eyes small, nearly round, never attaining anterior margin of face by one-fifth their greatest diameter and hind margin by about one-third; facets uniform. Orbits distinctly sunken, occiput swollen back of cheeks, with fine yellow hairs. Palpi tipped with brown; antennae about one and one-half times longer than head height. Third antennal segment basally swollen and covered with fine short velvety hairs. Arista pubescent, basally dark brown and swollen, remainder yellow.

Thorax: Brownish-yellow, notum centrally broadly black with three posterior black lines. Abundant fine yellow hairs, more numerous on dorsum. One pair dorsocentral and one distinct pair of scutellar bristles. Metanotum centrally blackened; mesopleura with cluster of fine yellow hairs posteroventrally. Sternopleuron ventrally darkened and with numerous fine yellow hairs. Legs lighter yellow than thorax becoming dark brown at tarsi. Posterior femora with indistinct apical brown spot. Wings hyaline, veins light brown; third and fourth longitudinal veins apically parallel, anal cell approximately equal to second basal. Halteres pale yellow.

Abdomen: Dark brown, sides toward base yellowish; with abundant yellow hairs. Genital clasper similar to *L. collaris* but spur arises laterally from clasper proper rather than medially, and degree of sclerotization is greater.

Length of body, 5 mm., wing, 5 mm.

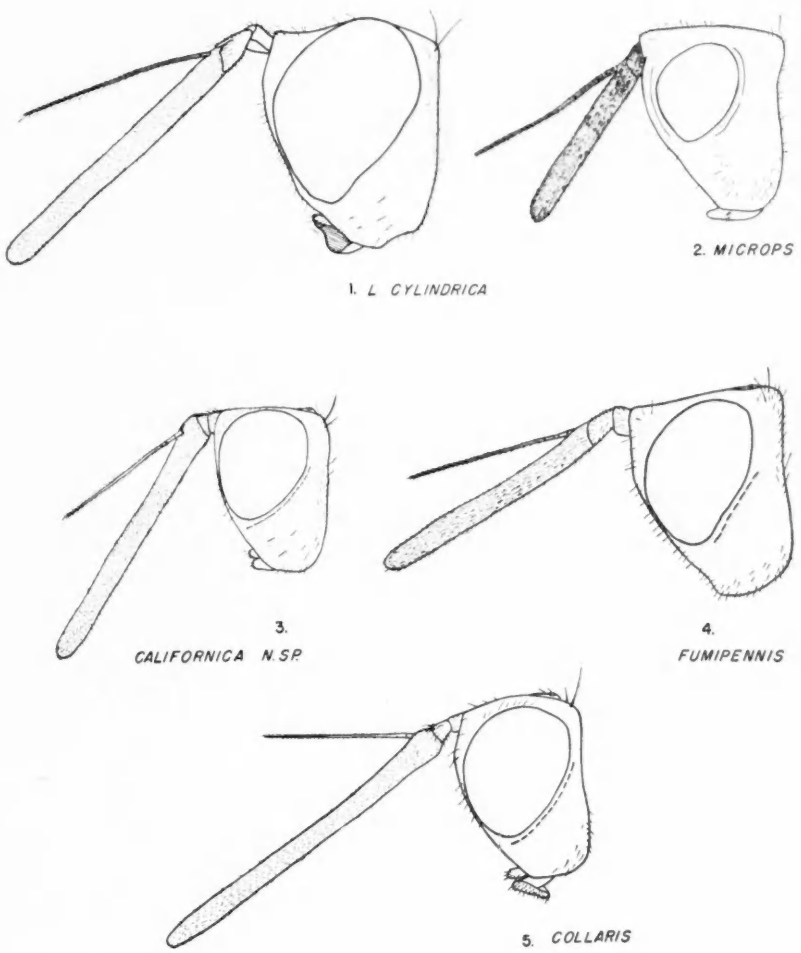
Female.—Herein described for first time.

Head: Yellow ocher with dusky brown area surrounding the dark brown ocellar triangle. Ocelli equidistant, anterior ocellus somewhat larger. Frontal triangle with marginal carinae which are absent behind; triangle attaining frontal suture and occupying about half of front at ocelli.

Eyes small, almost round, diameter slightly less than depth of cheek. Orbits distinctly sunken at periphery of eye. Occiput flattened. Antennal grooves very deep at sides, covered with fine, white hairs; median stripe polished, void of hairs beyond lower two-thirds. Palpi light brown. Antennae equal to head height, first segment partially concealed, second segment light brown, dorsolateral seam prominent, third segment dark brown and covered with fine, white pubescence. Arista pubescent; basally swollen, brown, apica two-thirds yellow. Arista almost reaching end of antenna.

Thorax: Yellow ocher except for one median brown stripe extending one-half length of dorsum, and two lateral brown stripes extending to middle half of dorsum. Metanotum centrally blackened. One pair prescutellar dorsocentrals and two apical scutellars, black. One pair of yellow supraalars. Dorsum covered with abundant fine yellow

PLATE I



Lateral view of head. FIG. 1, *Loxocera cylindrica;* FIG. 2, *L. microps;* FIG. 3, *L. californica;* FIG. 4, *L. fumipennis;* FIG. 5, *L. collaris.*

hairs. Mesopleura with a cluster of fine yellow hairs posteroventrally. Sternopleuron ventrally darkened and with numerous fine yellow hairs. Legs yellow ocher, becoming light brown at tarsi. Wings hyaline, veins light brown. Second basal and anal cells equal in length, anal vein not reaching wing margin. Halteres pale yellow.

Abdomen: Dark brown dorsally and apically, remainder yellow ocher, often laterally compressed, with fine yellow hairs. Ovipositor extended, blade-like, prominent.

Length of body, 6.5 mm., wing 4.5 mm.

Types.—Described from two male specimens from Paradise Valley, Mount Rainier, Washington, August, 1917, in collection of A. L. Melander. *Neallotype* female and two female *parallotypes*, Mount Rainier, Washington, August 10, 1941, L. J. Lipovsky. Neallotype and one parallotype at the State College of Washington, Pullman. One parallotype in Snow Entomological Collections, University of Kansas.

One male from Willow, Alaska, July 18, 1948 in United States National Museum, was taken during the Alaska Insect Project somewhere within the triangle of Anchorage, Fairbanks and Valdez. The exact location of "Willow" has not been determined.

Loxocera collaris Loew

Plate I, fig. 5; Plate II, fig. 6

Loxocera collaris Loew, 1869, Berliner Ent. Zeitschr., 13:184; Johnson, 1920, Psyche, 27: 17; Melander, 1920, Psyche, 27: 92.

This species is related to *Loxocera californica* described below but differs from it by the longer ocellar bristles which attain the margin of the eyes and the long converging inner vertical bristles. The anterior frontal region is more rounded when viewed in profile, third antennal segment is twice the length of the head, thorax and abdomen are a light yellow brown and median and lateral lines are absent from the dorsum.

The writer has seen only one male of this species. The description, therefore, is based primarily upon the female.

Male.—Somewhat darker than female, thorax and genae reddish-brown. Genital clasper stout with a distinct spur, similar to *L. californica.*

Length of body, 4–4.5 mm., wing, 3.5 mm.

Female.—Small, slender, light yellow species.

Head: Front dark chestnut brown, polished. Frontal triangle large, bare, attaining base of antennae, occupying more than half of front at widest area. Ocellar bristles long, attaining eye margins laterally. Inner verticals long, convergent, all but touching. Outer verticals strong. In profile, the anterior frontal region somewhat rounded. Antennal grooves deep, tapering toward oral margin, covered with fine, white pubescence. Median facial region dark brown, polished, with a slight median, carina. Palpi and proboscis light yellow, hairy. Genae light yellow with sparse yellow hairs. Eyes somewhat less than round, attaining anterior margin of face, orbits sunken ventrally. Width of eye, slightly greater than width

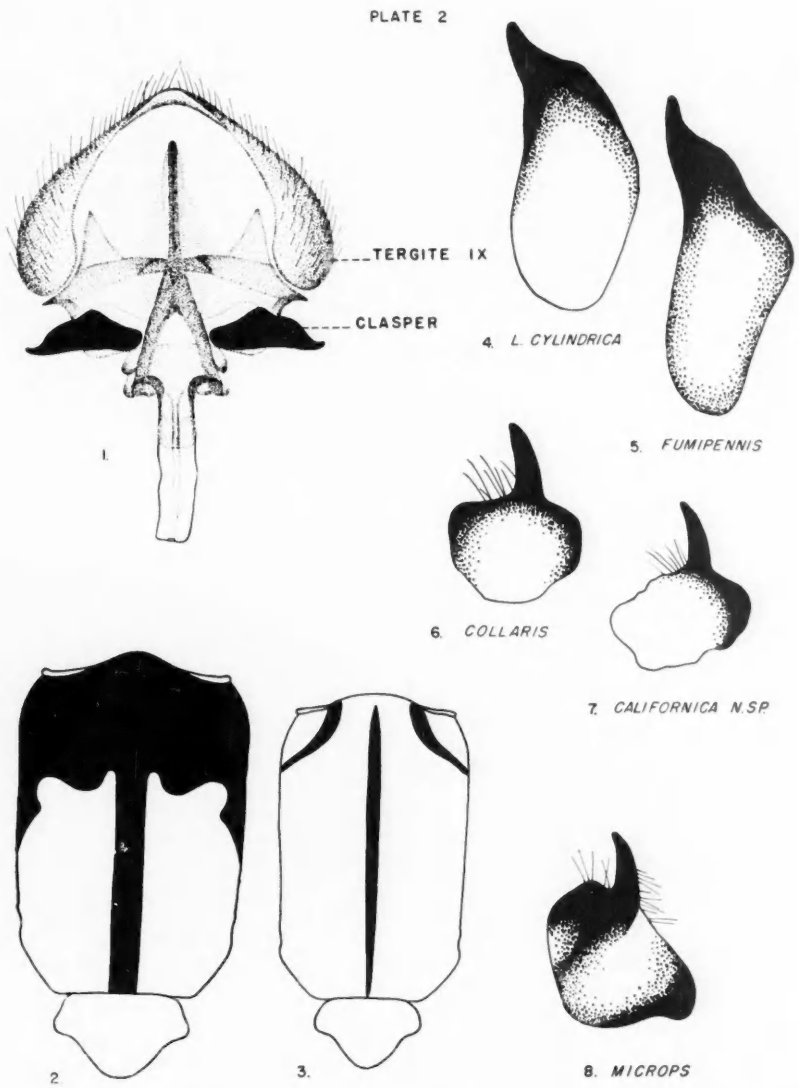


FIG. 1. Male genitalia of *Loxocera fumipennis*, ventral view, showing position of claspers. FIG. 2. *Loxocera cylindrica cylindrica*, dorsum of thorax, showing typical amount of black. FIG. 3. *Loxocera cylindrica pectoralis*, dorsum of thorax, showing typical amount of black. FIG. 4. *Loxocera cylindrica*, genital clasper. FIG. 5. *Loxocera fumipennis*, genital clasper. FIG. 6. *Loxocera collaris*, genital clasper. FIG. 7. *Loxocera californica*, genital clasper. FIG. 8. *Loxocera microps*, genital clasper.

of gena. Occiput rounded, dorsally darkened. Antennae except basally, dark brown, approximately twice length of face. First segment darkened, second segment and base of third, yellowish-brown. Third segment basally swollen and finely pubescent. Arista basally yellow, apically white, pubescent; equal to one half length of antenna.

Thorax: Anterior third of dorsum dark brown, polished. Remainder of thorax light yellow, hairy. Two pairs scutellar bristles, anterior pair weakened, one pair prescutellar dorsocentrals, two pairs supraalars, one pair presuturals, all black. Mesopleuron with ventral fringe of yellow hairs. Halteres whitish-yellow. Legs yellow, becoming darker at tarsi. Wings hyaline, veins yellow. Third and fourth longitudinal veins parallel towards the apex, posterior cross vein curved but not S-shaped, marginal cell slightly divergent toward apex.

Abdomen: Dark brown dorsally and ventrally toward apex, laterally yellow haired. Ovipositor prominent, blade-like.

Length of body, 5 mm., wing, 4 mm.

Types.—Holotype in Museum of Comparative Zoology, Cambridge, Massachusetts, taken in District of Columbia. Additional localities from Nova Scotia, Maine, New Hampshire, Massachusetts, New York, Connecticut, New Jersey, Virginia Wisconsin, Montana, Idaho, Washington, Oregon. Collection dates are from August 26 to September 14.

Loxocera californica, new species

Plate I, fig. 3; Plate II, fig. 7

This species is related to *Loxocera collaris* Loew, but is distinguished by the relatively short ocellar and inner vertical bristles, by the projection of the anterior frontal region, and a comparatively shorter third antennal segment. The thorax and abdomen are darker than *L. collaris* and median and lateral lines are present on the thorax. The body hair is longer and denser and specimens are of a smaller size.

Male.—Small, dark brown species with abundant body hairs.

Head: Front dark brown, polished. Face and occiput dark brown, genae and oral region light brown. Ocellar triangle elevated, distance from anterior ocellus to posterior ocelli greater than distance between the later. Frontal triangle large, polished, attaining anterior margin of front. Inner and outer vertical bristles strong, inner verticals convergent but never touching. Ocellar bristles extend about half the distance to eye margin laterally. In profile, the anterior frontal region projects. Antennal grooves distinct, covered with white pubescence. Median facial area with two lateral grooves and median carina which extends almost to oral margin. Proboscis and palpi light brown, with fine yellow hairs. Genae light brown, with sparse yellow hairs. Eyes small, almost round, attaining anterior margin of face. Orbits distinctly sunken posteroventrally. Width of eye almost equal to width of gena. Occiput rounded. Antennae one and one-half times as long as face, dark brown. First and second segments small and cup-shaped. Third segment long, swollen at base and covered with close fine yellow pubescence. Arista more than one-half length of antenna, also with fine, yellow pubescence, which is usually longer and sparser.

Thorax: Anterior one third of dorsum, two lateral and one median line, humeri, and dorsal third of mesopleuron, black. Median dorsal line sometimes broken, the three dorsal lines reaching almost to scutellum. Apex of scutellum and metanotum blackened. Remainder of thorax light brown. Two pairs of scutellar bristles, anterior pair weakened. Dorsum covered with fine yellow hairs. One pair prescutellar dorsocentrals, two pairs supraalars, one pair prealars, often broken. Mesopleuron with ventral fringe of decumbent yellow hairs. Halteres yellowish. Legs light brown covered with yellow hairs, becoming dark brown at tarsi. Wings hyaline, veins brown. Second basal and anal cells approximately equal. Anal vein not reaching wing margin. Third and fourth longitudinal veins only slightly arcuate, diverging slightly at apex. Posterior cross vein slightly S-shaped. Marginal cell of equal width throughout its length.

Abdomen: Entirely blackish-brown with abundant long yellow hairs. Often laterally compressed. Genital clasper similar to *L. collaris* excepting irregularity in outline and lesser degree of sclerotization.

Length of body, 4 mm., wing, 3.75 mm.

Female.—Differs in lighter yellowish-brown color of the genae. Front and dorsum are sometimes lighter in color than in male. Third antennal segment not noticeably swollen at base. Abdomen long, tapering, ovipositor extended, prominent.

Length of body, 5 mm., wing, 4.5 mm.

Types.—*Holotype* male, Sequoia National Park, California, August 6, 1940, R. H. Beamer. *Allotype* female and two male *paratypes*, Mono Lake, California, July 31, 1940, R. H. Beamer. Other *paratypes:* one female, Huntington Lake, California, July 15 (year not indicated) F. E. Blaisdell; one male Yosemite National Park, California, August 1, 1940, D. E. Hardy. Types and paratypes in Snow Entomological Collections, Lawrence, Kansas; a paratype in California Academy of Sciences, San Francisco, California.

Dr. R. H. Beamer tells me that the Mono Lake specimens were taken in the vicinity of Rush Creek near the southern shore of the lake. Thus they were probably from a humid meadow habitat rather than from an arid region like much of that surrounding Mono Lake.

Loxocera fumipennis Coquillett

Plate I, fig. 4; Plate II, fig. 5

Loxocera fumipennis Coquillett, 1901, Proc. U. S. Nat. Mus., 23: 617; Johnson, 1920, Psyche, 27: 17; Melander, 1920, Psyche, 27: 92.

This species is similar to *L. cylindrica* but is easily distinguished by the uniformly dusky wings. The eyes are somewhat smaller and never extend above the front when viewed in profile. The head is more triangular, the antennae comparatively shorter. Most specimens are considerably darker, being orange-red to rusty brown.

Male.—Head: Front dark brown, polished, bare. Frontal triangle darker, extending two-thirds distance to the antennal base, polished. Ocelli equidistant, ocellar bristles short, not extending beyond lateral margins of frontal triangle. Vertical bristles reduced. Posterior

orbital region dark brown. In profile, head appears triangular, anterior frontal region somewhat projecting, front dorsally flattened. Antennal grooves dorsally confluent, black, apically divergent, with white pubescence and a few light yellow hairs. Antennal grooves tapering off apically to form lateral slits at sides of oral cavity, yellow. Median facial region triangular, yellow, bare, gently convex. Palpi yellow, hairy, proboscis tipped with red, hairy. Genae light yellow almost void of hairs. Eyes ovate, attaining forward margin of face and dorsally often reaching front, but not extending above it in profile. Anterior orbits with fine white pubescence. Dorsal half of occiput dark brown, convex. Posteroventral orbital region not conspicuously sunken. Depth of eye equal to depth of gena. Antennae one and one-third times length of face. First antennal segment brief, second slightly longer with tinge of yellow, conspicuously bristled, third segment dark velvety brown, covered with silvery-brown pubescence. Third segment often constricted near apical third. Arista three-segmented, first segment dark brown, short, second slightly longer, yellow, third elongate, yellow. Pubescence of arista more closely appressed than in other species. Arista three-fourths length of third antennal segment.

Thorax: Anterior band, humeri, dorsal median and lateral lines, black; anterior band however frequently absent. Median line often extending to scutellum Metanotum with central black spot. Remainder of thorax deep orange-brown to orange-yellow. Apical scutellar bristles brief, anterior scutellars considerably weakened and inconspicuous. Prescutellar dorsocentrals weakened, one pair. Two pairs supraalars, distinct. Presuturals barely distinguishable from surrounding hairs. Dorsum covered with fine yellow to dark brown hairs. Mesopleuron with fringe of silvery decumbent hairs. Pleura with sparse, fine, yellow hairs. Halteres pale yellow. Legs orange-brown becoming black at tarsi. Wings comparatively short, uniformly dusky brown, veins dark brown. Anal cell slightly shorter than second basal. Characteristic weakening at basal third of wing is more conspicuous than in other species. Subcostal vein not confluent with first vein. Third and fourth veins parallel towards apex. Posterior cross vein bowed.

Abdomen: First segment with dorsal black spot, second with blackish-brown area, remainder becoming lighter in color towards apex which is orange-yellow. Ventrally concave. Genitalia inconspicuous. Genital clasper sinuate at posterior margin, apex fang-like in appearance, heavily sclerotized.

Length of body, 6 mm., wing, 4 mm.

Female.—Very similar to male. Ocellar bristles may extend beyond lateral margin of frontal triangle. Front often slightly concave. Apex of abdomen usually dark brown instead of orange-yellow. Ovipositor extended, blade-like.

Length of body, 7 mm., wing, 4 mm.

Types.—*Holotype* and *allotype*, Baldwin, Kansas, May, J. C. Bridwell, in United States National Museum, Catalogue No. 5507. Additional localities from North Dakota, South Dakota, Iowa, Colorado, Oklahoma, Arizona, Texas. Collection dates are from April 4 to September 11.

Loxocera cylindrica Say

Plate I, fig. 1; Plate II, fig. 4

This species varies considerably in size and color; it most closely resembles specimens of *L. collaris*. It is distinguished from *collaris* however by a relatively shorter antenna which is never more than one and one-half the head height. The wing tips are clouded with brown in varying degrees, and the eye in profile extends above the front.

Male.—Head: Front dark brown to orange yellow, usually lighter yellow laterally and toward anterior frontal region. Frontal triangle dark chestnut brown, reaching two-thirds to five-eights the distance to the antennal base. Ocelli equidistant, ocellar bristles moderately long, usually extending beyond lateral margin of frontal triangle. Vertical bristles present but often reduced. Anterior frontal region frequently depressed. Antennal grooves dorsally confluent, black pubescent, median facial triangle yellow, polished; apical grooves white-silvery to dark brown pubescent. Proboscis and palpi light yellow, hairy. Genae light yellow with sparse yellow hairs. Eyes large, ovate, extending above front when viewed in profile and attaining front margin of face. Eye width frequently twice that of gena. Occiput dorsally dark brown to black. Antennae never more than one and one-half times head height. First and second segments dark brown to yellow, bristled, third segment dark brown, velvety pubescent. Arista yellow with almost erect to moderately appressed yellow hairs. Arista two-thirds length of third antennal segment.

Thorax: Anterior margin yellow to one-half black, lateral and median lines present, black; median line often two-thirds width of scutellum. Humeri yellow to solidly black, scutellum yellow to light brown. Scutellar bristles moderate, anterior pair reduced. Prescutellar dorsocentrals very weak, supraalars strong, presuturals absent. Pleura completely yellow to one-half dorsally blackened, metanotum blackened. Remainder of thorax light yellow to yellow orange posteriorly. Halteres white to pale yellow. Legs light yellow becoming darkened toward tarsi. Hind femur often apically darkened. Wings hyaline apically clouded, especially around apex of third and fourth longitudinal veins and posterior cross vein. Veins yellow to brown. Apical cell slightly divergent.

Abdomen: First segment dorsally black, second sometimes black, remainder yellow to dark orange-red. Ventrally concave, genitalia inconspicuous.

Length of body, 5.5–7 mm., wing, 4.5–5.5 mm.

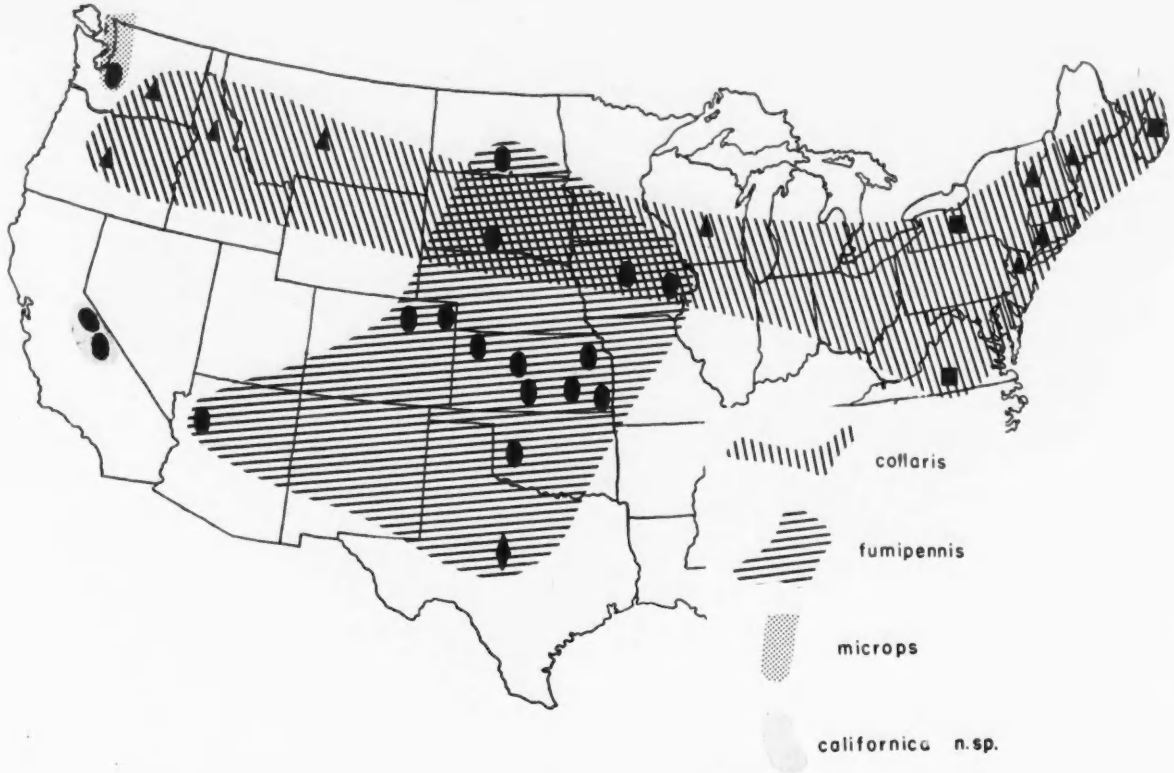
Female.—Very similar to male. Genae may appear light whitish-yellow. Wings sometimes less clouded and last abdominal segment dark reddish-brown and densely haired. Ovipositor extended, prominent.

Length of body, 6.5–8 mm., wing, 4.5–5.5 mm.

Loxocera cylindrica cylindrica Say

Plate II, fig. 2

Loxocera cylindrica Say, 1823, Jour. Acad. Sci. Philadelphia, 3: 98.
Loxocera pleuritica Loew, 1869, Berliner Ent. Zeitschr., 13: 38.



Map showing distribution of species from approximate collecting localities, exclusive of *L. cylindrica*. OVALS show *fumipennis, microps* and *californica* studied by the author. DIAMONDS shows *fumipennis* reported by Johnson and Melander. SQUARES show *collaris* studied by the author. TRIANGLES show *collaris* reported by Johnson and Melander. (The records given by these authors were listed as states only.)

Loxocera cylindrica var. *cylindrica*, Johnson, 1920, Psyche, 27: 15 (in part); Melander, 1920, Psyche, 27: 92 (in part).
Loxocera cylindrica var. *pleuritica*, Johnson, 1920, Psyche, 27: 15 (in part); Melander, 1920, Psyche, 27: 92 (in part).
Loxocera cylindrica var. *pectoralis*, Johnson, 1920, Psyche, 27: 15 (in part), new synonymy; Melander, 1920, Psyche, 27: 92 (in part).
Loxocera cylindrica var. *obsoleta* Johnson, 1920, Psyche, 27: 15 (in part); new synonymy; Melander, 1920, Psyche, 27: 92 (in part).

In this and the following subspecies the female is treated first because the subspecific characters are more apparent than in the male.

Female.—Larger, darker subspecies than *cylindrica pectoralis* (see Plate 4). Eyes distinctly swollen and bulging laterally from face. Dark band on pleura, if present, broken below the wing. Abdomen large, tergites distinctly separated. Thoracic markings brown to black. Posterior cross vein strongly convex.

Male.—Similar to female, occasionally smaller and lighter.

Types.—Type of *cylindrica* from Pennsylvania, presumably destroyed. Type of *pleuritica* from Connecticut at Museum of Comparative Zoology, Cambridge, Massachusetts. Types of *obsoleta* (two "types", one from Vermont, one from Massachusetts) in Museum of Comparative Zoology, Cambridge, Massachusetts. Additional localities from Montreal, Ontario, Quebec, New Brunswick, Maine, Vermont, New Hampshire, Massachusetts, New York, New Jersey, Maryland, North Carolina, Ohio, Indiana, Illinois, Wisconsin, Michigan, Minnesota, Iowa, Kansas.

These include localities reported by previous authors.

Loxocera cylindrica pectoralis Loew

Plate II, fig. 3

Loxocera pectoralis Loew, 1869, Berliner Ent. Zeitschr., 13: 38.
Loxocera cylindrica var. *cylindrica*, Johnson, 1920, Psyche, 27: 15 (in part), new synonymy; Melander, 1920, Psyche, 27: 92 (in part).
Loxocera cylindrica var. *pleuritica*, Johnson, 1920, Psyche, 27: 15 (in part), new synonymy; Melander, 1920, Psyche, 27: 92 (in part).
Loxocera cylindrica var. *pectoralis*, Johnson, 1920, Psyche, 27: 15 (in part); Melander, 1920, Psyche, 27: 92 (in part).
Loxocera cylindrica var. *obsoleta* Johnson, 1920, Psyche, 27: 15 (in part), new synonymy; Melander, 1920, Psyche, 27: 92 (in part).

Female.—Slender, elongate subspecies, usually paler than typical *cylindrica* (see Plate 4). Eyes not as distinctly swollen as in *cylindrica cylindrica*. Dark band on pleurae not broken below wings. Abdomen slender, elongate. Thoracic markings rusty-red. Posterior cross vein slightly S-shaped.

Male.—Occasionally smaller than female.

Types.—From Washington D. C. at Museum of Comparative Zoology, Cambridge, Massachusetts. Additional localities from Nebraska, Iowa, Illinois, Indiana, Missouri, Kansas, Arkansas, Texas, Louisiana, Pennsylvania, North Carolina, Virginia, New Jersey. These include localities reported by previous authors.

Loxocera quadrilinea Walker

Loxocera quadrilinea Walker, 1857, Trans. Ent. Soc. London, (2) 5: 329; Johnson, 1920, Psyche, 27: 17.

It is impossible to distinguish this species from any of the material before the author. Of this species Johnson says, "The identification of the species from the description is hopeless." Mr. Paul Freeman of the British Museum informs me that the type of *L. quadrilinea* Walker is not to be found and must be "presumed lost."

It is quite possible that the species belonged to some genus other than *Loxocera*.

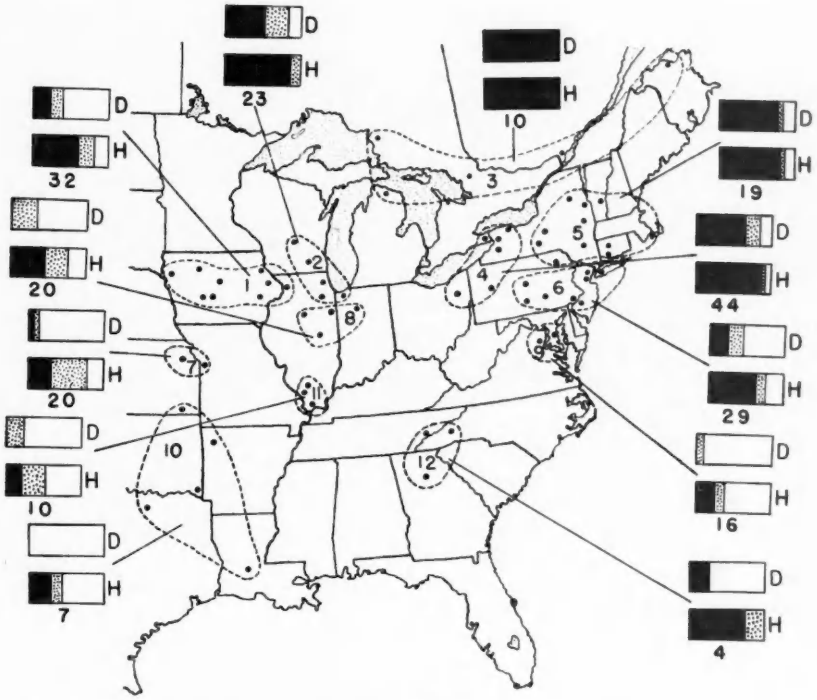
GEOGRAPHICAL VARIATION IN *Loxocera cylindrica* SAY

L. cylindrica is the most variable member of this genus. Previous workers have divided the species into four varieties, based entirely on color, a character shown in this study to be very inconstant. Examination of over two hundred and fifty specimens has shown every degree of intergradation possible. Examinations of genitalia have produced no correlation between their structure and the color markings. There is, however, a certain degree of correlation between coloration and distribution.

The map (Plate 4) shows the localities where individuals were taken, by dots, grouped into numbered areas by broken lines. The total number of specimens from each area is shown at the bottom of the respective block at the side of the map. The meaning of the shading of the blocks is given in the explanation of Plate 4. It will be noted that dark coloration is predominate in the north, especially the northeast, and that pale coloration predominates in the south except for a small group of specimens from the Appalachian highlands. However, a few pale specimens are found in all but the northeastermost populations, and occasional dark specimens are found far to the south. Thus great variability occurs over most of the range of this species.

The situation is parallel to that described by Kinsey (1930) for certain species of *Cynips* occurring in the eastern United States, and probably also to some of the variability described by Anderson (1949) in connection with introgressive hybridization of plants. It seems probable that such variability results from the meeting and interbreeding of populations which have been geographically isolated for some time. That is, a broad secondary zone of intergradation (in the sense of Mayr, 1942) has been formed. Just what geographical barrier may have isolated the northern and southern populations while one became extensively black, the other largely yellow, is not clear. In any case it is obvious that the line separating the darker, northern subspecies from the lighter, southern subspecies is now wholly arbitrary, because of complete intergradation between the two subspecies. If a line were to be drawn separating the two subspecies, it would probably extend westward through northern New Jersey and Pennsylvania, then southward to include the Appalachian Range and back through Ohio, Indiana, Illinois and northern Iowa. This division would place areas 2, 3, 4, 5 and 12 of Plate 4 in the northern zone and areas 1, 6, 7, 8, 9, 10 and 11 in the southern zone.

In the northern zone, typical conditions are shown in area 3, where both the dorsum and humeri are black in all ten individuals available for study. Area 5 shows that among nineteen individuals, 79% have the dorsum and humeri black, 5% have the dorsum and humeri inter-



Map showing distribution of the *L. cylindrica*.

Dots indicate collecting localities which are grouped into twelve numbered areas. The total number of individuals studied from each area is indicated beneath blocks on which are indicated certain characteristics of the individuals from each area.

The upper half of each block (D) represents the dorsum of the thorax. The color is indicated in terms of percentage of the total number of individuals available from the area, the horizontal length of each block representing 100%. Black indicates that the anterior one-fourth to one-half of the dorsum is dark (black to rusty). Stippled indicates that less than one-fourth of the dorsum is dark, while white indicates that the entire dorsum is yellow. Thus for area 2, 52 per cent of the individuals have one-half to one-fourth of the dorsum dark, 30 per cent have less than one-fourth dark, while 18 per cent have no dark areas on the dorsum.

The lower half of each block indicates by a similar method the coloration of the humeri. Black indicates that the humeri are dark, stippled indicates that they are intermediate, and white indicates that they are yellow.

mediate and 16% have the dorsum and humeri yellow or light. Of the southern zone, area 9 is perhaps most typical with a total of sixteen individuals. Dorsally none were black, 6% were intermediate and 94% were yellow. On the humeri, 25% were black, 12% intermediate and 63% yellow. It will be noted that nowhere do 100% of the individuals show humeri completely yellow.

The four specimens collected from area 12 show 75% with the humeri black, which is an exceptionally high percentage of black for the southern subspecific zone. These four individuals, however, were taken from the southern extent of the Appalachian Range in an ecological region probably more closely allied to the northern subspecific zone than to the immediate surrounding area.

It is worthy of note that in addition to the two characters whose variation is detailed in Plate 4, other features show similar variability within populations and similar geographic variation. Northern specimens, especially the black northeastern ones, are usually larger than southern ones. They also tend to have more black on the legs and abdomen than southern specimens.

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At the International Congress of Entomology at Amsterdam, foundations were laid for the development of an International Union for the study of social insects, the term being interpreted to include not only termites and social Hymenoptera, but also other insects which exhibit social phenomena. The French Section has organized to the extent of issuing a bulletin on a provisional basis, until the international organization can be officially established and can begin its official publication. Its *Bulletin* has made a good start; in addition to setting forth the background and aims of the proposed organization, it has included a short original article on the "group effect" in insects, together with a digest of current publications by members of the Union.—M. T. J.

SECOND REPORT ON THE PERFORMANCE OF EUROPEAN CORN BORER PARASITES IN DELAWARE[1]

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The principal purpose of this report is to evaluate the activities of exotic and native parasites of the European corn borer, *Pyrausta nubilalis* (Hbn.), in Delaware during the past five years (1947–1951), and to summarize briefly the performance record for each species. The earliest releases of the introduced species were made in 1941 and 1943 by the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture. In 1944, this undertaking became a cooperative operation on the part of the Bureau and the Department of Entomology of the Delaware Agricultural Experiment Station. Liberation of parasites continued through 1946. A report covering all releases, as well as parasite recoveries between 1943 and 1947, was made by MacCreary and Rice (1949). Most of this information has also been published annually by the Bureau in Special Supplements of the Insect Pest Survey (1946, 1947, 1948, and 1949). In 1947, the Bureau devised a plan of obtaining a 50-borer sample of hibernating larvae from the center of sections 10 miles square. This was followed in making the collections discussed in the present report.

Attention is called to the data on the 1947 samples from Kirkwood (New Castle County) and Stockley (Sussex County) given in Table III and previously published in Insect Pest Survey Special Supplement No. 5 (1948) and by MacCreary and Rice (1949). These collections were in addition to the statewide 10-square-mile survey. They are the last for the two original colonization points in the State and are a part of a study of parasite dispersion. The average parasitism for these localities is 17.6 percent. This is considerably above that of 11.6 percent procured from the square-section survey of the same year. None of the information obtained from these colonization points in 1947 is utilized in this report for analyzing parasitism, because it was not gathered in the same manner. However, it is included for the purpose of emphasizing that two types of surveys were made in that

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[2]Assistant Research Professor, Entomology.

[3]Live borers were collected in 1947 by Donald MacCreary; in 1948, by J. C. Warren; in 1949, by J. G. Davis; and, in 1950 and 1951, by H. E. Milliron.

[4]The writer acknowledges the assistance rendered by the laboratory of the United States Department of Agriculture, Bureau of Entomology and Plant Quarantine at Moorestown, New Jersey, where, under the supervision of D. W. Jones, all collections were processed for parasites, and by K. D. Arbuthnot in supplying most of the records included herein.

year. If the percentages of average parasitism recorded in both cases are combined, the total percentage for all species is increased from 11.6 to 15.2 and that for the dominant one, *Lydella stabulans grisescens* R. D., from 11.5 to 15.

Conforming to the Bureau survey plan, the State was divided into 30 sections, the border ones in all cases comprising less than 10 square miles. Each year, beginning in 1947, a fall sample of approximately 50 live borers was collected from near the center of each section and submitted to the Moorestown, New Jersey, laboratory for parasite processing. While results for 1947 were given in the report by MacCreary and Rice (1949), they are also included herein for a more complete analysis of all parasite recoveries resulting from the standard survey procedure. Data for the period 1947–1951 are presented by counties in Table I, summarized for the State as a whole in Table II, and shown graphically in Figure 1.

A total of 150 collections, comprising 6,544 borers, was made. Parasites were reared from all except three samples—one in 1947 and two in 1949. In 1947, the average total parasitism slightly exceeded 11 percent, and was about equal in each of the three counties. The following year, it had nearly doubled in New Castle County, and was about three times higher in the remaining two counties. In 1949 it dropped to about the 1947 level in Kent and Sussex Counties, but remained high (32 percent) in New Castle. Borer destruction by parasites increased again in 1950 to 46 percent in New Castle; to 29 percent, in Kent; and to 22 percent, in Sussex. Parasite activity declined somewhat in 1951 in all counties. Average total parasitism for the five years was 28 percent in New Castle; 22 percent, in Kent; and 18 percent, in Sussex. The percentage for the entire state was lowest in 1947 (11.6 percent), highest in 1948 and 1950 (30–31 percent), with a 22 percent average for the period (see Table II).

It is difficult to correlate the single effect of parasites on borer populations from year to year, when the complex action and/or interaction of other factors, aside from weather, are not considered as an integral part of parasite or borer-abundance surveys. This opinion was clearly set forth by Baker and Bradley (1938), and a survey technique that could accomplish this correlation is still unavailable. If parasitism alone was the factor controlling borer populations, it would then be reasonable to assume that the host population in a given locality would be diminished considerably following a season of heavy parasitism. This is not always the case, as the following data with respect to host abundance and parasite activity in Delaware indicate:

	Borers per 100 Plants	Total Percent Parasitism
1947	66	12
1948	91	30
1949	70	15
1950	36	31
1951	85	22
1952	133	..

Only in 1948–1949 does there appear to be some direct correlation; during the remaining years, borer populations increased in spite of the high rate of parasitism. There can be little doubt, however, that a

parasite, for example *L. s. grisescens*, which destroys annually a great many borers figures prominantly in reducing populations of its host. With the present information, the possibility of arriving at any positive and consistant correlation of this single effect on the host seems remote.

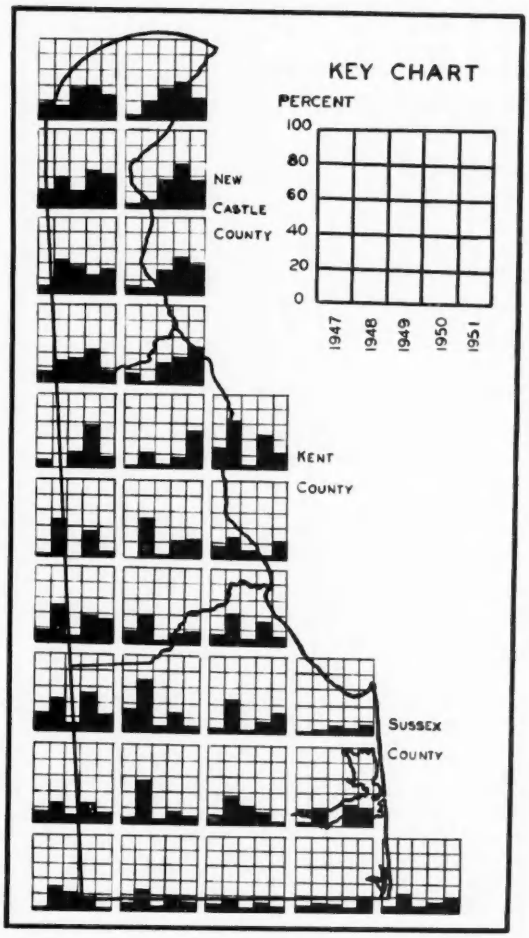

FIG. 1. Parasitism of the European Corn Borer by all species as determined by surveys, Delaware, 1947 to 1951 inclusive. Since *Lydella s. grisescens* was responsible for 99 percent of the total parasitism, this is essentially a figure for that species.

SUMMARY OF PERFORMANCE OF EXOTIC SPECIES

Analysis of all data obtained in Delaware since 1943 indicates that a single species, *Lydella stabulans grisescens* R. D., has not only become well established, but is now widely dispersed and has attained a state of

TABLE I

PARASITISM OF HIBERNATING EUROPEAN CORN BORERS IN DELAWARE, 1947–1951, INCLUSIVE
(By counties)

COUNTY AND YEAR	NUMBER OF		NUMBER AND PERCENTAGE PARASITIZED BY							
	Sections Sampled	Borers Observed	*L. s. grisescens*		*M. gifuensis*		*P. penitalis*		All Species	
New Castle County										
1947	8	366	40	10.9	1	0.3	.....	.....	41	11.2
1948	8	379	75	19.8	4	1.1	2	0.5	81	21.4
1949	6	244	77	31.6	2	0.8	.....	.....	79	32.4
1950	8	337	152	45.7	.....	.....	.....	.....	152	45.7
1951	8	361	114	32.8	2	0.5	1	0.3	117	33.6
Period	38	1687	458	27.1	9	0.5	3	0.2	470	27.9
Kent County										
1947	8	359	41	11.4	.....	.....	.....	.....	41	11.4
1948	8	354	132	37.3	.....	.....	.....	.....	132	37.3
1949	12	497	58	11.7	.....	.....	.....	.....	58	11.7
1950	8	356	104	28.5	.....	.....	1	0.4	105	28.9
1951	8	308	79	25.3	.....	.....	.....	.....	79	25.3
Period	44	1874	414	22.1	.....	.....	1	0.05	415	22.1
Sussex County										
1947	14	656	78	11.9	.....	.....	.....	.....	78	11.9
1948	14	565	181	32.0	.....	.....	.....	.....	181	32.0
1949	12	554	57	10.3	.....	.....	.....	.....	57	10.3
1950	14	631	128	21.4	1	0.1	.....	.....	129	21.5
1951	14	654	99	15.1	.....	.....	.....	.....	99	15.1
Period	68	3060	543	17.7	1	0.03	.....	.....	544	17.7

equilibrium with its environment in each of the three counties. Moreover, its activity, measured in terms of the destruction of borers, far overshadows that of all other species combined. *Macrocentrus gifuensis* Ashm. also has become established, principally in northern Delaware, but its value is almost insignificant in comparison. Recovery of the remaining introduced species has been either negative or negligible. A recent report by Cory *et al.* (1952) describes a similar record of performance for these parasites in Maryland.

The activity of each species is discussed hereinafter, particularly with regard to recoveries during the past five years. Evaluations are based entirely on fall collections of overwintering larvae. They do not indicate, necessarily, the true effectiveness or the total absence of an

TABLE II

PARASITISM OF HIBERNATING EUROPEAN CORN BORERS IN DELAWARE, 1947–1951, INCLUSIVE (SUMMARIZED)

YEAR	NUMBER OF		NUMBER AND PERCENTAGE PARASITIZED BY							
	Sections Sampled	Borers Observed	*L. s. grisescens*		*M. gifuensis*		*P. penitalis*		All Species	
1947	30	1381	159	11.5	1	0.1	.....	.....	160	11.6
1948	30	1298	388	29.9	4	0.3	2	0.2	394	30.4
1949	30	1295	192	14.8	2	0.2	.....	.....	194	15.0
1950	30	1247	384	30.8	1	0.08	1	0.08	386	30.9
1951	30	1323	292	22.1	2	0.15	1	0.07	295	22.3
Period	150	6544	1415	21.6	10	0.15	4	0.06	1429	21.8

introduced species. Such information can only be procured by similar collections of first-generation borers earlier in the season. Certain species, for example *Horogenes punctorius* (Rom.), appear to be more efficient parasites of first-generation borers in some localities. This was well expressed, for that species, by Baker *et al.* (1949). The same might be true of *L. s. grisescens*, especially in some years. Another species, which should be mentioned in this respect, is *Sympiesis viridula* (Thoms.); because of its interesting ectoparasitic habit, the effectiveness of its activity may not be properly established through the usual fall surveys. Arbuthnot (1950) has pointed out that only those parasite larvae that are present at the time of survey are observed, whereas attack on the host is continuous throughout the season. Furthermore, parasite pupae are sometimes found in borer tunnels some distance from the host remains and, thus, might not be encountered by the surveyor. During July of 1952, a considerable amount of parasitism was observed in Delaware on second and third-instar borers by an undetermined hymenopterous parasite not recorded in any of the recent fall collections. This could possibly have been the result of the activity of either *H. punctorius* or *Chelonus annulipes* Wesm., both of which are at present regarded as of no value in this State.

Lydella stabulans griescens R. D.

This is a fly of the family Larvaevoridae. It was introduced into the United States from Europe in 1929 and, also, from the Orient in the same year. The first small consignment was liberated in Delaware in 1941 at Stockley in Sussex County; followed, in 1943, by a lot at Kirkwood in New Castle County. Further liberations were made in 1944 at two additional points in both New Castle and Kent Counties; and another lot, in 1946, in Kent; making a total of 3,179 specimens (MacCreary and Rice, 1949). It was recovered first in the 1943 collections at Kirkwood and Stockley, where it destroyed 3 percent of the borers at the former location, and 15 percent at the latter. It established itself quickly and firmly at all colonization points. Baker

TABLE III

PARASITISM OF HIBERNATING EUROPEAN CORN BORERS IN DELAWARE AT TWO COLONIZATION POINTS USED FOR DISPERSION STUDY (1947)

Location	Number of		Number and Percentages Parasitized by							
	Samples Collected	Borers Observed	*L. s. grisescens*		*M. gifuensis*		*C. annulipes*		All Species	
Kirkwood	22	1006	185	18.4	4	0.4	1	0.1	190	18.9
Stockley	25	1003	164	16.4	.....	.....	.....	.....	164	16.4
Totals and Averages	47	2009	349	17.4	4	0.198	1	0.047	354	17.6

et al. (1949) gave a maximum rate of dispersion of about two miles in the Lake States area and conclude that this is "probably much faster in parts of the East," which appears to have been the case in Delaware. Data reported by MacCreary and Rice (1949) from the local study of dispersion show the parasite to have been present three to five miles from the original release point two years following initial liberation.

This parasite has proved to be the most valuable species from the time it was introduced. It was recovered from all except 13 of 141 fall collections, comprising 8,049 borers, made from 1943 to 1946, inclusive. Ten of these negative collections were made in 1945, a year when the average parasitism by this species (calculated from 55 samples including 3,105 borers) amounted to less than 8 percent. A total of 197 fall collections, consisting of 8,630 borers, was made from 1947 to 1951, inclusive. This parasite was recovered from all these collections except four. It has accounted for 99 percent of the total parasitism during the past five years. Its efficiency in destroying borers has varied from year to year, and from collection to collection, the lowest percentage being 1.9 in one sample from Kirkwood in 1947, and the highest 69.7 in a single collection from Sussex County in 1948. Borer control attributed to it from 1947 through 1951 amounted to 21.4 percent.

When making collections, the presence of parasite puparia (entire and empty) has been recorded. In many cases, such data suggest that parasitism of first-generation borers is higher than that of the second.

A hyperparasite, ***Eupteromalus nidulans*** (Thoms.), was encountered on a few occasions, but never in sufficient numbers to cause concern.

Macrocentrus gifuensis Ashm.

This parasite belongs to the hymenopterous family Braconidae. It was imported originally into the United States from Europe in 1920 and again, from Korea and Japan, in 1929. First releases were made in all Delaware counties in 1941. Data supplied by MacCreary and Rice (1949) show that 81,789 individuals were liberated from 1941 to 1946, inclusive, or more than five times as many as all other introduced species combined. Initial recoveries were made in a collection at Hockessin, and another at Milton in 1945; at the former location three specimens were recovered and, at the latter, but a single specimen. Although this species had become established by 1945, it has since maintained itself at a low level of density. No more than 45 specimens have been recovered from 12 of the 338 borer-collections. The percentage of borers destroyed by *M. gifuensis* has always been low, except in 1946, usually amounting to only a fraction of one percent. In one exceptional borer collection made that year at Hockessin in northern Delaware, where this parasite has been most active in destroying its host, it was responsible for 51.4 percent of the total parasitism, or slightly greater control than that accomplished by *Lydella*, which at that time was generally not very effective.

During the five-year period under discussion, this species was recovered from five collections consisting of 241 borers, and killed from 1.9 to 8.9 percent (average 4.1 percent). However, it has been responsible for destroying only 0.15 percent of all borers collected in the State. The value of this parasite in Delaware appears to be negligible, although it has proved beneficial in other parts of the Country, especially in Massachusetts.

Chelonus annulipes Wesm.

This parasite, also a hymenopterous species of the family Braconidae, was imported from Italy in 1929. The first release in Delaware was made in 1944 at Hockessin. In 1945, lots were liberated at Kirkwood, Dover, and Stockley, and an additional number at the latter point in 1946. In all, 2,229 specimens were released from 1944 to 1946, inclusive (MacCreary and Rice, 1949). Only a single individual has ever been recovered, in a collection in 1947 at Kirkwood. Recent surveys have given no evidence of its occurrence.

Horogenes punctorius (Rom.)

This hymenopterous parasite belongs in the family Ichneumonidae. It was imported into the United States from Europe in 1921 and, from the Orient, in 1930. A total of 3,959 specimens was released in Delaware at Kirkwood, Dover, and Stockley from 1944 to 1946, inclusive (MacCreary and Rice, 1949). One specimen of *H. punctorius* was

recovered on the Eastern Shore of Maryland in 1947, according to Cory *et al.* (1952). The species has never been collected in this State, and probably is not established here. However, it is important in some sections of the United States, notably in Massachusetts, where for several years it was the dominant parasite of the European corn borer, later superseded in abundance by *M. gifuensis*.

Sympiesis viridula (Thoms.)

This European hymenopterous parasite, of the family Eulophidae, was imported into the United States from Italy in 1930, but was not released in Delaware until 1946, when lots of 2,000 each were liberated at Kirkwood, Dover, and Stockley. Although it has been recovered in the Lake States (Baker *et al.* 1949), it has never been found in this State or elsewhere in the East.

SUMMARY OF THE PERFORMANCE OF NATIVE PARASITES

Agathis agilis (Cress.)

Six specimens of this braconid parasite were reared from collections at Stockley in 1945. It has never been taken in any subsequent collections and appears to be of little or no value in controlling the European corn borer.

Cremastus minor Cush.

A single specimen of this hymenopterous parasite of the family Ichneumonidae was obtained in 1946 (MacCreary and Rice, 1949). It has never reappeared and must be considered as a rare parasite of the European corn borer.

Pyraustomyia penitalis (Coq.)

This dipterous parasite belongs in the family Larvaevoridae. Three specimens were recorded in 1946 from Kirkwood and one, in the same year, from Frederica. No specimens were obtained from the 1947 collections. Two individuals were reared in 1948 from one New Castle County collection, but these amounted to only two-tenths of one percent of the total percentage for the State. None occurred in the 1949 collections. Only a single specimen was obtained in 1950 and again in 1951, in both years amounting to one-tenth of one percent of the total parasitism. It is obvious that this parasite has been of negligible value in controlling the European corn borer in Delaware.

SUMMARY

Five species of exotic parasites have been released in Delaware to aid in the control of the European corn borer. Of these, *Lydella stabulans grisescens* R. D. has become firmly established throughout the State. It is the only species of importance. The percentage of borers destroyed during the years 1947 to 1951, inclusive, has ranged from 12 to 31, with an average of 22. A second species, *Macrocentrus gifuensis* Ashm. is established in northern Delaware, but is of little

value since it has destroyed only a fraction of one percent of all borers collected during the past five years. The remaining three species do not appear to have established themselves.

Native parasites kill at most only an insignificant number of borers. The destruction of borers by the most prominent of these, *Pyraustomyia penitalis* (Coq.), has not exceeded one-tenth of one percent within recent years.

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CHEMICAL CONTROL OF INSECTS, BY T. F. WEST, J. ELIOT HARDY, and J. H. FORD. xi+211 pages, 44 figs. John Wiley and Sons, Inc., New York. January, 1953. Price, $3.25.

The authors of this book have endeavored to survey the development of modern insecticides. In this endeavor they have crammed much more into the 211 pages. Well over half of the text has been devoted to a discussion of the "older" insecticides, an outline of pest control, repellents and attractants, and very brief treatment (5 pages) of weed control.

It appears that the manuscript for this book was prepared long before the actual date of publication. Numerous important recent research findings have been omitted. Many of the insecticides now accepted as an integral part of present crop protection are referred to as "preliminary." The literature cited at the end of each chapter contains few references beyond 1946.

TABANIDAE ATTRACTED TO LIGHT[1]

S. W. FROST
The Pennsylvania State College

It is not generally known that horseflies (Tabanidae) come rather freely to light. Slingerland (1902) mentioned a single unidentified species of *Chrysops* that came to a light trap. Philip (1931) reported collecting a few specimens at a street light. MacCreary (1940) was the first fully to realize the importance of light in obtaining Tabanidae. He took 10 species and 412 specimens at New Jersey light traps equipped with 25 watt lamps. These came to single traps located at four light houses in Delaware Bay. Among them were five species of *Tabanus*, one species of *Leucotabanus* and four species of *Chrysops*.

TABANIDAE TAKEN FROM A SINGLE TRAP OPERATED FROM MAY 15 TO SEPTEMBER 15 AT YORK SPRINGS, PENNSYLVANIA

Species	No. Males	No. Females
Tabanus sulcifrons Macq.	11	38
Tabanus pumilus Macq.	4	3
Tabanus sparsus milleri Whitney	5	12
Tabanus reinwardtii Wied.	0	1
Tabanus lasiophthalmus Macq.	0	1
Tabanus nigrescens Palisot	1	1
Tabanus quinquevittatus Wied.	1	1
Tabanus lineola scutellaris Walk.	0	4
Atylotus bicolor Wied.	1	0
Chrysozona rara (John.)	1	2
Chrysops nigra Macq.	0	2
Chrysops geminata Wied.	1	6
Chrysops vittata Wied.	1	4
Chrysops wiedemanni Kröber	0	6
Chrysops moecha O. S.	0	1
Chrysops beameri Brem.	0	1
Chrysops celer O. S.	1	0
Total.	27	83

Although Haddow (1950) did not use lights, he reported that some Tabanidae fly just after sundown and many fly all night long.

In operating New Jersey light traps at various localities throughout Pennsylvania, the writer has long realized that the Tabanidae are attracted to light. The numbers of Tabanidae are frequently small and, in the presence of large numbers of other insects, are often overlooked. During 1951, one trap, operated in a highly cultivated fruit

[1]Authorized for publication on December 28, 1951, as paper No. 1714 in the Journal Series of the Pennsylvania Agricultural Experiment Station.

area at York Springs, Pennsylvania, yielded an amazing number of species and individuals. The trap was adjacent to a small pond and apparently in a favorable location. It was the only trap, among six operated in other localities the same year, that yielded a significant number. Although only a relatively few specimens were saved from this trap, which ran from May 15 to September 15, 17 species and 110 individuals were obtained. These were identified by Dr. L. L. Pechuman.

In addition to those mentioned in the preceeding table, two species, *Tabanus sackeni* Fairch., and *Chrysops univittatus* Macq., were taken in light traps in other Pennsylvania localities. Dr. L. L. Pechuman, in correspondence, informs me that long series of both sexes of *Tabanus sackeni* have been collected at light at Ithaca, New York.

When searching for methods of sampling insect population, the number of individuals and species obtained by any method is important. Heretofore, female Tabanidae, which are blood suckers, were obtained chiefly by human or animal bait while the males, which visit flowers, were considered difficult to secure. The information to date indicates that males and females can be secured at light in fair numbers. The light trap seems to be an answer to the survey problem.

From the standpoint of health, the proportion of males and females taken at light is important. Based on 10 species and 412 specimens taken from four widely separated light traps, MacCreary found that 59 per cent of the catch were females. The writer's figures, based on 17 species and 110 specimens, all from a single trap, indicate that 74 per cent were females.

It is evident, if light traps are operated in areas where Tabanidae are present, large numbers of species and individuals can be expected. Contrary to general opinion, many Tabanidae are nocturnal in habit and the males and females come to light rather freely.

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ERRATUM

In the December, 1952, ANNALS, vol. 45, p. 617, line 7 of the book review, "male aphids" should read "maple aphids."

THE ANT LARVAE OF THE SUBFAMILY FORMICINAE[1]

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The Formicinae are generally regarded as the most highly specialized subfamily of ants, surpassing even the Dolichoderinae, which are close competitors. Their larvae, however, range from generalized to highly specialized—from the Melophorini to the Oecophyllini and Camponotini. By contrast the larvae of the Dolichoderinae constitute a homogeneous group and are all highly specialized by reduction.

In this article we describe the larvae of 64 species representing 18 of the 45 genera and 10 of the 12 tribes. All known references in the literature are cited bringing the total considered up to 117 species representing 23 genera.

Subfamily **Formicinae** Lepeltier

Thorax and first abdominal somite forming a more or less distinct neck which is rather stout and curved ventrally; rest of abdomen stouter, straight and subellipsoidal; posterior end round. Anus terminal or subterminal. Leg vestiges usually distinguishable. Thirteen differentiated somites. Integumentary spinules restricted, minute and arranged in transverse rows. Body hairs moderately numerous to abundant, short, uniformly distributed; alveolus and articular membrane usually lacking. Body-hair shapes varied; a species usually has two or three types; the most common types are (1) branched (branches two to many), (2) denticulate and (3) simple. Head neither large nor small; broader than long. Antennae minute to moderate in size, each mounted on a low convexity and bearing three sensilla. Head hairs few to abundant; short to long; rarely denser or longer than body hairs; alveolus and articular membrane present. Head hairs varied; a species usually has one or two types; the most common shapes are (1) branched (generally two or three branches); (2) denticulate and (3) simple. Usually there are hairs between the antennae. Labrum small to moderate-sized; bilobed or subparabolic; broader than long; narrowed ventrally; anterior surface bearing sensilla and minute hairs; posterior surface with sensilla and minute spinules; these spinules arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally. Mandibles small to moderate-sized; ratio of head width to mandible length = 2.3–5.5 (average 3); ratio of mandible length to mandible width at base = 1.2–1.7 (average 1.4). Moderately sclerotized; subtriangular in anterior view; wedge-shaped, with the edge medial or with the basal third somewhat thick and the rest thin and blade-like; apex forming a small blunt smooth tooth which is slightly curved medially; medial teeth absent or vestigial; anterior and posterior surfaces with longi-

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tudinal and/or oblique ridges, which occasionally may bear spinules. Maxillae usually swollen ventrolaterally; apex conical, conoidal or paraboloidal and directed medially; spinules generally restricted to the apex or the medial surface; palp small, typically a skewed peg with five sensilla; galea finger-like with two apical sensilla. Labium with anterior surface spinulose; palp typically a low knob bearing five sensilla; opening of sericteries wide and salient, with two projections. Hypopharynx densely spinulose, the spinules minute and in numerous subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle.

Alderz, 1886:—The form of the woolly hairs ("ullhåren") characterizes the "Camponotidae" (p. 51). "Camponotid larvae have comparatively larger heads than Myrmicid larvae and the anterior corner of the first segment's ventral side is in the former large and projecting" (p. 52). Internal anatomy: pp. 59–64. "Uncinate hairs are single-hooked. Larvae moderately active" (p. 277). (Translation from the Swedish by Professor Edith E. Larson.)

Athias-Henriot, 1947:—"Tous les Camponotinés ont une tête grande à pièces développées. Elles sont relativement très mobiles" (p. 251). "Les *Camponotinés* ont des larves mobiles, a tête bien différenciée, à pièces buccales bien développées" (p. 253). Internal anatomy: pp. 258, 261 and 263 and Fig. 2 on p. 255. "Formicinés.—Les larves sont très primitives, avec un type anatomique très uniforme. Sous-famille très homogène. On peut toutefois classer les genres dans l'ordre suivant: 1. *Acantholepis*, 2. *Plagiolepis* et *Camponotus*, 3. *Categlyphis*, ce qui correspond á l'ordre suivi habituellement pour les adultes" (p. 268).

Bischoff, 1927, p. 384:—The larvae are fed with liquid food from the crops of the nurses.

Brun, 1924, p. 95:—"Die Fütterung wird . . . gewöhnlich in der Weise vorgenommen, dass die fütternde Arbeiterin einen Tropfen Nahrungsflüssigkeit aus ihrem Kropfe ausbricht und denselben auf den Mund der Larve fallen lässt."

Emery, 1925, p. 6:—"La nidification des *Oecophylla*, de quelques espèces de *Camponotus* d'Amérique et de la plupart des *Polyrhachis*, faite au moyen de la soie produite par leurs larves, m'a surtout frappé. Il m'a semble impossible d'expliquer ce fait si extraordinaire par une simple convergence d'instincts; il est beaucoup plus vraisemblable que *Oecophylla*, *Camponotus* et les genres dérivés de celui-ci (entre autres *Polyrhachis*), aient eu un ancêtre commun, dont ils ont hérité cet instinct. La plupart des *Camponotus* l'ont perdu, à mesure que se développait le polymorphisme si remarquable de ce genre et la nidification dans le bois ou dans la terre. De même, quelques *Polyrhachis* du sous-genre *Chariomyrma*, qui habitent sous les écorces ou sous les pierres."

Forel, 1921:—"Les larves, quoique souvent mobiles, sont presque toujours alimentées directement par dégorgement du contenue du jabot de l'ouvrière qui les nourrit" (p. 24). (=1928, Vol. I, p. 24: "The larvae, although often mobile, are nearly always directly fed by the regurgitation of the contents of the nurses' crop.") "Les larves sont en général un peu plus mobiles que chez les *Dolichoderinae*"

(p. 140). (=1928, p. 234: "The larvae are generally a little more mobile than those of the Dolichoderinae.")

Forel, 1922:—"Les larves de quelques . . . *Camponotinae* sont nourries directment par leur ♀, qui leur dégorgent le contenu de leur jabot." (p. 136). (=1928, Vol. I, p. 517: "The larvae of some . . . Formicinae are directly fed by their ♀, which disgorge to them the contents of their crops.")

Gantes, 1949, p. 88:—"Chez les . . . Formicidés . . . nous voyons une évolution nette: . . . *Formica, Lasius, Cataglyphis* sont les plus primitifs: larve néonate nue ou presque, mandibule bien développée et très coupante, poils de la larve adulte très serrés. Larves agiles. *Plagiolepis, Camponotus*, sont plus évoluées: les larves sont moins agiles. Je ne les pas vues manger seules. Les mandibules sont plus massives. Les poils plus clairsemés. Chez les deux on trouve des poils en crosse chez les jeunes larves."

Kellogg, 1905, p. 541:—"The character and amount of the food given the larvae is carefully controlled by the workers."

Wheeler, 1900, p. 27:—"The worker ants can control the production of individuals like themselves and of individuals like their queen. It is further maintained that these differencés are effected by the quantity and quality of the food administered to the larvae at a certain period of their development; but here our knowledge ends."

Wheeler, 1920, p. 48:—The trophorhinium may function as a stridulatory organ, "when the food supply is exhausted, and thus apprise the worker nurses of the larva's hunger." Many genera of Formicinae "also have elaborate but coarser stridulatory surfaces on the mandibles, so that the larva may be able to produce a variety of sounds and therefore apprise the nurses of more than one need or craving."

Wheeler, 1937, p. 38:—The larvae of the Formicinae are fed by a "careful administration *per os* of liquid food regurgitated from the nurse's crop."

KEY TO THE MATURE FORMICINE LARVAE IN OUR COLLECTION

1. Chiloscleres present . . . . . **TRIBE CAMPONOTINI**
   Without chiloscleres 2
2. Thorax noticeably more slender than the abdomen and forming a neck which is arched ventrally 3
   Not as above 10
3. Maxillary apex papillose . . . . . **TRIBE MELOPHORINI** 4
   Maxillary apex not papillose 5
4. Body hairs all denticulate . . . . . **Melophorus**
   Body hairs branched or with fuzzy tips . . . . . **Notoncus**
5. Hairs short simple spikes . . . . . **TRIBE GESOMYRMICINI**
   Hairs not as above 6
6. Head hairs numerous, denticulate, long, whip-like . . . **TRIBE GIGANTIOPINI**
   Head hairs not as above 7
7. Mandibles conspicuously broad; apical tooth abruptly marked off . . . . . **TRIBE FORMICINI** 8
   Mandibles not as above . . . . . **TRIBE PLAGIOLEPIDINI** 9
8. Body hairs with bifid tips (a few may have denticles on the branches) . . . . . **Formica**
   Body hairs of several types (simple, branched, denticulate) . . . . . **Lasius**

9. Body hairs of two types (smooth and denticulate); mandibles with a conspicuous jagged notch at the middle of the mesal border.....**Plagiolepis**
Body hairs of three types (smooth, denticulate and branched); mesal border of mandibles with a few denticles.....**Acropyga**
10. Hairs simple, mostly minute.....11
Branched hairs present.....12
11. All hairs minute, simple and acute.....**TRIBE OECOPHYLLINI**
Most hairs minute; a band of long whip-like hairs on the dorsa of thoracic somites II and III and abdominal somites I–VI.....
.....**TRIBE MYRMELACHISTINI**
12. Mandibles with a short apical tooth and a small subapical tooth.....
.....**TRIBE PRENOLPIDINI** 13
Mandibles with a long slender apical tooth; no subapical tooth.....
.....**TRIBE BRACHYMYRMYICINI**
13. Body constricted near the middle; head hairs simple.....**Prenolepis**
Body not constricted near the middle; head hairs branched.....**Paratrechina**

Tribe **Melophorini** Forel

Shaped somewhat like a crookneck squash (*i.e.*, thorax and first abdominal somite forming a moderately long and rather slender neck which strongly curves ventrally; rest of abdomen elongate, somewhat swollen and straight.) Anus subterminal. Cranium subhexagonal in anterior view. Head hairs few. Labrum bilobed. Maxillary apex papillose. Anterior surface of labium with a median protuberance near the base.

Genus **Melophorus** Lubbock

Shaped somewhat like a crookneck squash; thorax and first abdominal somite forming a moderately long and rather slender neck which is strongly curved ventrally; rest of abdomen elongate, somewhat swollen and straight, with the dorsal profile convex and the ventral nearly straight. Anus subterminal. Body hairs abundant and very short; of only one type: slender, slightly curved and with the basal half smooth, the distal half denticulate. Head small; cranium subhexagonal in anterior view. Antennae with two sensilla each. Head hairs few, moderately long and shaped like body hairs. Labrum bilobed; posterior surface with about seven sensilla. Maxillae large and lobose; apex papillose. Labium with a median protuberance on the anterior surface near the base.

Melophorus bagoti Lubbock

(Pl. I, figs. 1–5)

Shaped somewhat like a crookneck squash; thorax and first abdominal somite forming a moderately long and rather slender neck which is strongly curved ventrally; rest of abdomen elongate, somewhat swollen and straight, with the dorsal profile convex and the ventral nearly straight. Ventral surface somewhat flattened. Lateral longitudinal welts feebly developed. Slightly attenuated toward the posterior end which is round. Anus subterminal. Thirteen differentiated somites. Integument of anterior portion of prothorax spinulose, the spinules minute and in transverse rows. Body hairs abundant and uniformly distributed; basal half smooth, distal half denticulate; slender and slightly curved; slightly stouter on the ventral surface of the thorax; no alveolus or articular membrane; very short (length 0.1–0.25 mm.).

Head small; cranium broader than long, subhexagonal in anterior view. Head hairs few, slender, slightly curved; basal half smooth, distal half denticulate; moderately long (0.076–0.126 mm.); with alveolus and articular membrane. Antennae with two sensilla each. Labrum bilobed, due to a deep median incision of the ventral border: breadth twice the length; anterior surface with about eight sensilla near the ventral border and with four or five hairs on each lobe; posterior surface spinulose, the spinules minute and arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; about seven sensilla on the posterior surface. Mandibles robust and moderately sclerotized; width at base two-thirds the length; the basal three-fourths stout and wedge-shaped, the edge medial; narrowing to a slender apical tooth which is smooth, round-pointed and slightly curved medially and posteriorly; anterior and posterior surfaces roughened with numerous subparallel ridges which are mostly longitudinal. Maxillae large and lobose; the rounded apex furnished with numerous papillae; palp a skewed peg, with two apical, one subapical and two lateral sensilla; galea finger-like, with two apical sensilla. Labium with a median protuberance near the base of the anterior surface; the anterior surface spinulose, the spinules minute and isolated; palp a skewed peg with two apical and four lateral sensilla; opening of sericteries a small shelf in a shallow depression on the end of the labium. Hypopharynx densely spinulose, the spinules arranged in subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: 16 larvae from Central Australia.)

The larva of this species is unusually interesting for two reasons. First, it belongs to the most primitive genus of the Formicinae. Second, it resembles very closely the larvae of the lower Ponerinae; in fact, it might almost be placed in the genus *Ectatomma*.

Wheeler, G. C., 1938:—No wing rudiments (p. 141); vestigial gonopods of eighth and ninth abdominal somites present but those of the seventh apparently lacking (p. 142).

Genus **Notoncus** Emery

Shaped somewhat like a crookneck squash; thorax and first abdominal somite forming a moderately long and rather slender neck which is strongly curved ventrally; rest of abdomen elongate-subellipsoidal. Anus subterminal. Body hairs moderately numerous; of three types: (1) short, 4- to 6-branched, with the branches all in one plane and long hairs, (2) some branched, (3) some fuzzy-tipped, arranged in bands, one band around the middle of each somite. Antennae small. Head hairs few and short, with the tips fuzzy. Labrum bilobed; narrowed ventrally; posterior surface with 12 small and three large sensilla on each lobe. Maxillae small and narrow; apex papillose and directed subventrally; palp chair-shaped. Labium with a median spinulose protuberance on the anterior surface near the base.

Notoncus foreli Ern. André

(Pl. I, figs. 6–11)

Shaped somewhat like a crookneck squash; thorax and first abdominal somite forming a moderately long and rather slender neck,

which is curved ventrally; rest of abdomen elongate-subellipsoidal. Lateral longitudinal welts feebly developed. Leg vestiges present. Anus subterminal. Thirteen differentiated somites. Integument of the ventral surface of the thorax and abdominal somite I with short transverse rows of minute spinules. Body hairs moderately numerous and uniformly distributed; without alveolus and articular membrane. Of three types: (1) most hairs short (0.07–0.1 mm.), 4-to 6-branched, with the branches all in one plane; around the middle of each somite is a narrow band of about a dozen long (0.21–0.25 mm.) hairs, (2) some branched, (3) most with fuzzy tips. Cranium subhexagonal in anterior view; broader than long. Head hairs few, short (0.035–0.07 mm.); the tips fuzzy; alveolus and articular membrane present. Antennae small, mounted on low convexities; each with three (sometimes two) sensilla. Labrum bilobed due to a deep median incision of the ventral border; breadth 1.75 × length, narrowed ventrally; anterior surface of each lobe with four hairs and a few small sensilla; posterior surface densely spinulose, the spinules minute and arranged in rows which converge toward the dorsal corners; posterior surface of each lobe with 12 small and three large sensilla. Mandibles moderately sclerotized; width at base two-thirds the length; the basal three-fourths stout and wedge-shaped, with the edge medial; narrowing to a smooth, slightly curved apical tooth, which is variable in length and sharpness; a small blunt tooth on the mesal border at the base of the apical tooth; anterior and posterior surfaces roughened with numerous oblique subparallel ridges. Maxillae small and narrow; apex directed subventrally, conoidal, its integument papillose; palp-chair-shaped, with two apical and three lateral sensilla; galea finger-shaped, with two apical sensilla. Labium with a median anterior prominence near the base, which is furnished with minute spinules arranged in short transverse rows; palp a short peg with two apical and two lateral sensilla; opening of sericteries a transverse slit on the anterior surface. Hypopharynx spinulose, the spinules exceedingly minute and arranged in long subtransverse rows. (Material studied: several larvae from Victoria, courtesy of Mr. W. L. Brown; and six damaged integuments of head and thorax from South Australia.)

Genus **Myrmecorhynchus** Ern. André

Myrmecorhynchus emeryi Ern. André

Wheeler, 1917, p. 17:—" *Young Larva.* Body plump, with distinct segments, constricted behind the prothoracic segment, which is large and swollen. Head rather small, broad, and rounded, covered with sparse, simple hairs, without antennae and with short maxillae and labium furnished with the usual truncated sense-papillae. Mandibles small, flattened, falcate, with long apical tooth and blunt denticles along the inner border. Surface of body covered with flexuous, 2-, 3-, or 4-branched hairs, except the ventral thoracic surface, which is beset with simple, bristly hairs. *Adult Larva.* Body much swollen, but with distinct segments. Head extremely small. Hairs almost lacking, except on the head and ventral surface of the anterior segments, where the hairs are short, simple, and bristly. The shape of the larva suggests that it does not spin a cocoon but forms a naked pupa." Pl. I, fig. 4:

a, young larva in side view; *b* and *c*, branched hairs of same; *d*, adult larva; *e*, head of same in anterior view; *f*, mandible of same.

Tribe **Plagiolepidini** Forel

Genus **Plagiolepis** Mayr

Thorax forming a short stout neck which is strongly arched ventrally; abdomen elongate, rather slender, straight and subcylindrical. Anus ventral. Body hairs short to rather long, the shorter denticulate, the longer whip-like. Cranium subheptagonal in anterior view. Head hairs few, moderately long and denticulate. Labrum small and not bilobed. Mandibles small; basal half broad; distal half forming a long, slender, round-pointed tooth; a conspicuous jagged notch at the middle of the mesal border. Maxillae rather narrow and short, with the apex paraboloidal and directed ventrally.

Gantes, 1949:—"*Plagiolepis*, *Camponotus* sont plus évoluées: les larves sont moins agiles. Je ne les pas vues manger seules. Les mandibules sont plus massives. Le poils plus clairsemés. Chez les deux on trouve des poils en crosse chez les jeunes larves" (p. 88). Les poils en crosse "chez la larve néonate sont répartis sur le dos et tout autour du bout de l'abdomen, puis aux stades suivants on ne les a plus que dorsalement et sur les derniers segments abdominaux. Chez la larve adulte il n'y en a plus (*Camponotus*), ou très peu (*Plagiolepis*)" (p. 87).

Plegiolepis (**Anoplolepis**) **longipes** (Jerdon)

(Pl. I, figs. 19–23)

Thorax forming a short stout neck, which is strongly arched ventrally. Abdomen elongate, rather slender, straight, subcylindrical; diameter greatest at the fifth abdominal somite, diminishing gradually toward the anterior end and more rapidly toward the posterior end, which is round-pointed. Lateral longitudinal welts feebly developed. Anus ventral. Thirteen differentiated somites. Body furnished with a uniform and moderately abundant covering of short to rather long hairs, some of which are denticulate, slightly curved and 0.05–0.12 mm. long, while others are simple, whiplike and longer (about 0.16 mm.); no alveolus or articular membrane. Cranium subheptagonal in anterior

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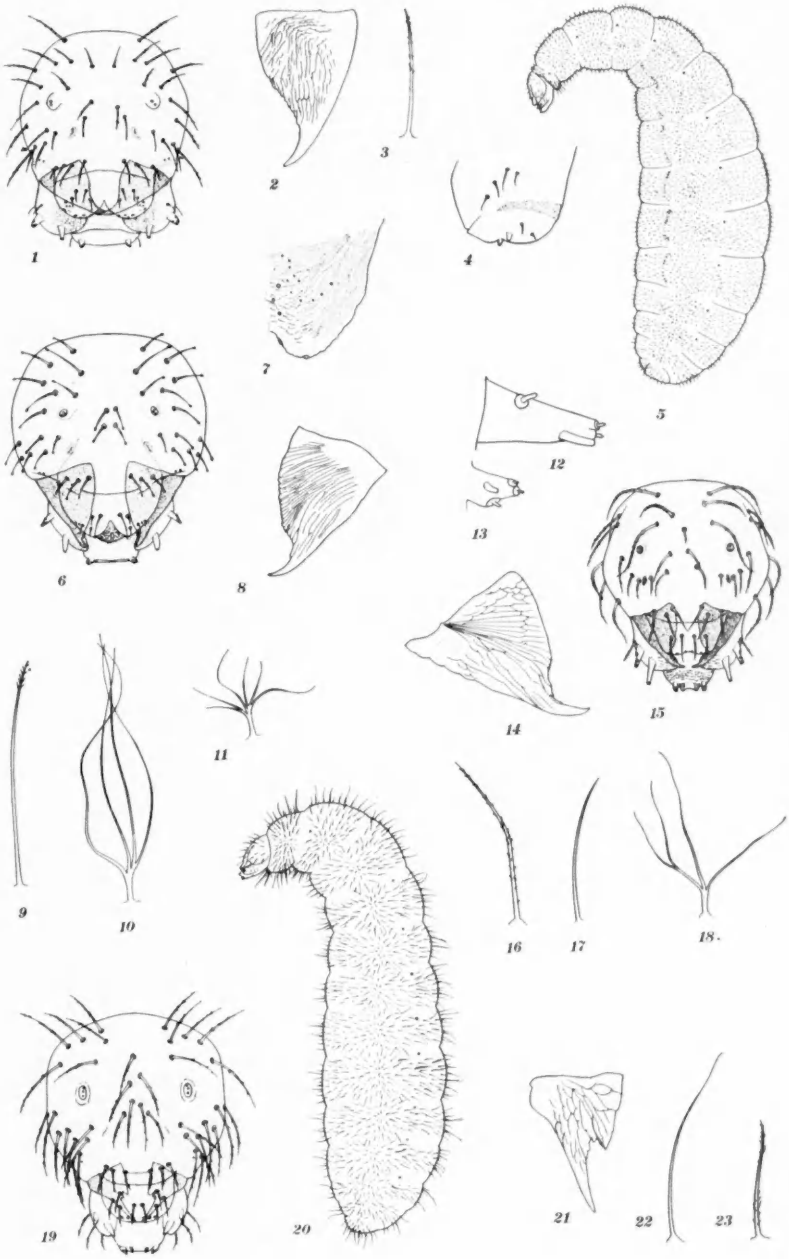
EXPLANATION OF PLATE I

Melophorus bagoti Lubbock, Figs. 1–5. 1, head in anterior view, ×44; 2, left mandible in anterior view, ×95; 3, body hair, ×113; 4, labium in side view, ×44; 5, larva in side view, ×4.

Notoncus foreli Em. André, Figs. 6–11. 6, head in anterior view, ×57; 7, right half of labrum in posterior view, ×118; 8, left mandible in anterior view, ×95; 9 and 10, two long body hairs, ×121; 11, short body hair, ×121.

Acropyga moluccana papuana Mann, Figs. 12–18. 12, maxillary palp in anterior view, ×371; 13, labial palp in anterior view, ×371; 14, right mandible in anterior view, ×185; 15, head in anterior view, ×76; 16–18, three body hairs, ×95.

Plagiolepis (*Anoplolepis*) *longipes* (Jerdon), Figs. 19–23. 19, head in anterior view, ×95; 20, larva in side view, ×20; 21, right mandible in anterior view, ×185; 22 and 23, two body hairs, ×185.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view, about as broad as long. Head hairs few, long (0.07–0.1 mm.) and denticulate; with alveolus and articular membrane. Antennae with three sensilla each. Labrum small, breadth at base 1.5 × the length, ventral margin entire and convex, ventral corners broadly rounded; anterior surface with about eight hairs and with six sensilla near the ventral border; posterior surface spinulose, the spinules minute and arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; posterior surface with six sensilla near the middle. Mandibles small, moderately sclerotized; basal half broad; distal half forming a long, slender, smooth, round-pointed tooth; a conspicuous jagged notch at the middle of the mesal border; anterior and posterior surfaces roughened with longitudinal ridges. Maxillae rather narrow and short with the apex paraboloidal and directed ventrally; palp a skewed peg bearing two apical and three lateral sensilla; galea digitiform, bearing two apical sensilla. Labial palp a skewed peg bearing two apical and two lateral sensilla; opening of sericteries wide and saliant. Hypopharynx densely spinulose, the spinules arranged in subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: six larvae from the Philippine Islands.)

Emery (1899, p. 8) described the larvae of *longipes* as *squisitamente ortocefalo:* the head and mouth parts differed little from those he had observed in *Camponotus vitreus*. Pl. II, fig. 10*a*, larva in side view; *b*, head in side view, enlarged.

Goot, 1915 (we have translated from the Dutch original):—"The just hatched larva is elongate-oval, with the anterior end distinctly tapering and the posterior end broadly rounded. The head is very small, pointed and rather distinct. The body somites are marked off by shallow grooves. At this stage the larva is entirely naked and its color is glassy white. Its length is ±0.53 mm., its breadth ±0.21 mm. At first the larva develops slowly. As with the eggs, the young larvae are held together in packets, which are carried about by the workers. On such occasions apparently the workers also feed the larvae with small drops of liquid food which they regurgitate and press against the mouth of the larva. After about nine days, when the length has reached 0.96 mm. and the breadth 0.26 mm., the first (?) molt occurs, after which the outward appearance of the young larva is altered. The head and thorax are furnished with a rather large number of fine, moderately long hairs; the abdomen is still naked. The larvae are still in packets. . . . At the end of four days another molt occurs, . . . after which the abdomen is provided with numerous fine long hairs. The length is now 1.94 mm., the breadth 1.70 mm. . . . The larvae are no longer in packets but separate and in groups on the floor of the nest; there they are provided with food. Only when alarmed do the workers pick up and carry about the larvae of this size. During this last stage of its development the larva grows remarkably but still keeps its elongate bottle-like shape. About six days after the last molt it is fully grown. . . . Its length is now about 3.1 mm., its breadth 0.78 mm. It now loses what scant mobility is had previously and the color becomes more grayish and opaque. . . . It is carried by the workers to a place where it can find points of attachment for spinning

its cocoon. . . . In artificial nests this is preferably in the vicinity of a pile of pupae; if these are wanting, the workers cover the larva with bits of refuse, such as fine particles of earth, pieces of empty cocoons, fine threads, granular excrement, etc. This debris affords points of attachment for the first threads of the cocoon. The spinning of the cocoon is exclusively a larval function; by regular movements of the head the product of its spinning glands is fashioned into an opaque leathery cocoon, which is usually completed in one day. The last larval molt now occurs and the pupa emerges inside the cocoon" (pp. 4–5). The average life cycle is given (pp. 4–6) as: egg 19–20 days; larva 19 days; worker pupa in the rainy season 20–22 days (dry season 16–17 days); total two months. Table II (p. 10) shows the duration of the larval stage in 27 individuals.

Goot, 1916 (we have translated from the Dutch original):—"This queen larva may be distinguished from the worker larvae by its remarkable size: fully grown it is about 7 mm. long and 3 mm. broad. The body shape is that of the worker larva; the whole body is hairy but the hairs are relatively shorter. Pupation is similar to that of the worker larva" (p. 5). He referred (p. 5) to his 1915 study of the life cycle, which is given here as: egg 18–20 days, larva 16–20 days; pupa 20 days; total 50–65 days. Plate I is a photograph of eggs, larvae and cocoons.

Plagiolepis (Anoplolepis) custodiens (F. Smith)

Generally similar to *longipes*, except for larger body size and relatively smaller head. (Material studied: 10 queen larvae from the Congo.)

Plagiolepis (Plagiolepis) crozi Santschi

Athias-Henriot (1947, p. 251) states that the larva is very similar to that of *Camponotus barbaricus*. The head is less massive, the maxillae form much more distinct lobes. Dorsally the fourth, fifth and sixth somites bear crozier-shaped hairs. Fig. 1 on page 251 shows a larva in side view. Internal anatomy is discussed on pages 257, 260 and 266. On page 260 the larva is said to be omnivorous.

Gantes, 1949:—"Les larves ont la même forme en très petit [que celles de *Lasius niger*]. La tête diffère légèrement: le labre est formé d'un seul lobe qui recouvre entièrement les mandibules. Sur la face dorsale, on a trois poils sur chaque côté. Les mandibules se voient par transparence sous le labre. Elles sont très petites, simple triangle brun clair de 0 mm. 08, dont la base s'insère dans la tête. Tout le corps est couvert de poils simples, très fins et très courts" (p. 77). On Plate II are shown labrum, hairs and mandible of this larva. "En général, les larves adultes sont de taille inférieure ou égale aux ouvrière. Rarement, elles sont plus grandes comme chez *Plagiolepis crosi*" (p. 87). Growth is discussed on pp. 85 and 86. See also under the following species.

Plagiolepis (Plagiolepis) pygmaea (Latreille)

Gantes (1949):—"Chez *Plagiolepis pygmaea* on retrouve les mêmes sortes de poils que chez *Lasius*, mais en beaucoup plus petit; poils épineux, poils bifurqués uniquement dans la region anale et des poils

en crosse sur les segments 4 et 5 dorsalement. Enfin dan ce genre, j'ai une larve de sexué ♀ qui est plus grosse. La tête est semblable à celle de l'ouvrière. Elle diffère surtout par les poils: sur les segments de l'abdomen, dorsalement, on trouve des poils à double crochet, fins et longs, 0 mm. 25; sur les côtés de l'abdomen nous avons de longs poils terminés par une fourche. Il est curieux de voir le *P. pygmaea*, espèce européenne très voisine du *P. crosi* nord-africain, muni d'une pilosité larvaire notablement plus variée" (pp. 77–78). "D'une façon générale, des espèces voisines d'un même genre peuvent avoir des larves bien distinctes (par exemple *Plagiolepis crosi* et *pygmaea*)" (p. 89).

Gösswald (1934/5, pp. 120 and 125) cited *pygmaea* as a host of a mermithid and inferred that the nematode larva might have been parasitic in the ant larva.

Genus **Acropyga** Roger

Body hairs abundant and short; of three types—(1) denticulate, (2) 2- to 6-branched and (3) simple. Cranium subhexagonal in anterior view. Antennae small; each with two sensilla. Head hairs few, long and stout, of two types: (1) smooth and (2) denticulate. Maxillae with the apex paraboloidal and directed medially; palp a slender subcone, with five sensilla, each of which bears a peg. Labial palp a short skewed peg, with five sensilla, each of which bears a peg.

Acropyga moluccana papuana Mann

(Pl. I, figs. 12–18)

Body hairs abundant and rather uniformly distributed; short (0.16–0.25 mm.); no alveolus or articular membrane. Of three types: (1) simple hairs; (2) denticulate hairs: (3) branched hairs, with three to six (mostly four) branches which have long flexible tips. Integument with scattered short transverse rows of minute spinules. Cranium slightly broader than long, subhexagonal in anterior view. Head hairs few, long (0.08–0.2 mm.) and stout: denticulate or smooth; alveolus and articular membrane present. Antennae small, each mounted on a lobose protuberance: with two sensilla. Labrum bilobed due to a slight impression of the ventral border; narrowed ventrally; twice as broad (at base) as long; anterior surface of each lobe with two short hairs and with two sensilla near the ventral border; posterior surface spinulose, the spinules minute and arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; three sensilla on each half of the posterior surface. Mandibles moderately sclerotized; basal three-fourths stout and subtriangular; distal fourth a long, smooth, sharp-pointed apical tooth, which is curved medially; surface of base roughened with numerous ridges which are mostly longitudinal. Maxillae slightly swollen ventrolaterally; the apex paraboloidal and directed medially; palp a slender subcone with two apical and three lateral sensilla, each of which bears a conspicuous peg; galea digitiform, with two apical sensilla. Anterior surface of the labium roughened with short transverse rows of minute spinules; palp a short skewed peg with two apical and three lateral sensilla; each bearing a conspicuous peg; opening of sericteries wide and salient, with two projections. Hypopharynx densely spinulose, the

spinules minute and arranged in subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: four damaged integuments from the Solomon Islands.)

Acropyga moluccana Mayr

Generally similar to *papuana*, but with three types of body hairs: (1) 2- to 4-branched, with 2-branched the most abundant type on the dorsum, 0.10–0.16 mm. long; (2) simple, long and flexuous, the most abundant type on the venter, 0.1–0.35 mm. long; (3) a few denticulate, 0.04–0.16 mm. long. (Material studied: a single immature larva from Java.)

Acropyga (Rhizomyrma) fuhrmanni Forel

Weber, 1944:—"The larvae are moderately slender and have numerous hairs, some of which are simple, some trifid and some flattened and finely divided apically; these are lacking at the sutures" (p. 97). Fig. 6 on Plate I shows a larva in side view and two hairs.

Acropyga (Rhizomyrma) paramaribensis Borgemeier

Bünzli, 1935:—"Die Larven sind reichlich behaart, etwas schwächer am Vorderende und an der Bauchseite. Die Haare erreichen eine Länge von .18 mm und lassen oft unregelmässige Verzweigungen erkennen; später brechen Teilstücke ab, wohl wegen des häufigen Transportes der Larven durch die Arbeiterinnen. Von den larvalen Mundwerkzeugen heben sich die hakenförmigen, kurzen, etwas pigmentierten. Mandibeln am deutlichsten ab" (p. 519). Fig. 32 on p. 517 shows a worker larva in side view and hairs.

Genus **Acantholepis** Mayr

Acantholepis frauenfeldi Mayr

Athias-Henriot (1947) discusses internal anatomy on pages 254, 256, 260, 263, 265 (Fig. 5) and 266. The larvae are carnivorous(p.260).

Bernard (1948, p. 107):—"Larves couvertes de poils courts, droits; loin de s'accrocher au sable, elles roulent sur lui quand on ouvre de terrier." Internal anatomy and its relation to economy of water is discussed.

Tribe **Myrmelachistini** Forel

Genus **Myrmelachista** Roger

Straight and subcylindrical, diameter nearly uniform back to the fifth abdominal somite, then tapering rather rapidly to the posterior end, which is round-pointed; anterior end broadly rounded; no neck; head applied to the anteroventral surface. Anus terminal. Segmentation indistinct. Body hairs of two types: (1) minute spikes, which are generally distributed; (2) long whip-like hairs in transverse rows on the dorsal surface of mexothorax, metathorax and abdominal somites I-VI (one row each). Cranium subheptagonal in anterior view. Antennae with two sensilla each. Head hairs few, simple and minute. Labrum bilobed. Mandibles small and feebly sclerotized; base very broad; distal fourth forming a slender straight sharp-pointed tooth.

Maxillae rather small; palp a low discoid, with five sensilla, three of which bear each a slender peg; galea a low knob bearing two sensilla. Labium small.

The larvae of this genus certainly do not fit in the Formicinae, but resemble more closely the larvae of the Dolichoderinae, notably *Azteca*.

Myrmelachista (Decamera) zeledoni Emery

(Pl. II, figs 1–6)

Straight and subcylindrical, rather stout, diameter nearly uniform back to the fifth abdominal somite, then tapering rather rapidly to the posterior end, which is round-pointed; anterior end broadly rounded; no neck; head applied to the anteroventral surface. Anus terminal. Leg vestiges present. Segmentation indistinct. Body hairs few; large intersomitic area naked on the dorsal surface and also on the ventral surface of the thorax; no alveolus or articular membrane. Of two types: (1) minute spikes (0.009–0.027 mm.), which are uniformly distributed over the hairy areas of the body; and (2) long (about 0.13 mm.) whip-like hairs arranged in transverse rows on the dorsa of mesothorax, metathorax and abdominal somites I-VI (one row each). Cranium subheptagonal in anterior view with the corners broadly rounded; breadth 1.5 × the length. Hairs of head few, minute (0.009–0.012 mm. long), simple and slightly curved; arrangement and number variable; alveolus and articular membrane present. Each antenna mounted on a low convexity and bearing two sensilla. Labrum short; breadth three times the length; narrowed ventrally; bilobed due to a shallow impression of the ventral border; anterior surface with three or four hairs on each lobe; posterior surface densely spinulose, the spinules minute and arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; posterior surface with two clusters of three sensilla each near the middle. Mandibles small; feebly sclerotized; wedge-shaped, with the edge medial; subtriangular in anterior view; base very broad; distal fourth smooth, slender, straight and sharp-pointed; medial half of anterior and posterior surfaces roughened with numerous longitudinal ridges. Maxillae rather small; palp a low discoidal projection with five sensilla, three of which bear each a slender peg; galea a low knob with two apical sensilla, each of which bears a spinule. Labium small; palp a low knob with about five sensilla some of which bear each a spinule; opening of sericteries a short transverse slit on the anterior surface. Hypopharynx densely spinulose, the spinules arranged in subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: 11 larvae from Costa Rica.)

Myrmelachista (Myrmelachista) ambigua ramulorum Wheeler

Similar to *zeledoni* but differing in the following details: Body hairs about half as numerous. Breadth of labrum about twice the length; about five hairs on the anterior surface. (Material studied: eight damaged integuments from Culebra Island.)

Tribe **Brachymyrmicini** Emery

Genus **Brachymyrmex** Mayr

Stout and rather short; thorax curved ventrally to form an extremely short stout neck; abdomen straight; diameter greatest at the third abdominal somite, diminishing gradually toward either end. Posterior end narrowly rounded. Anus subterminal. Segmentation indistinct on the posterior half. Body hairs sparse and short; of three types: (1) mostly 3- to 5-branched, a few longer whip-like hairs on the dorsal surface of the abdomen which are either (2) simple or (3) bifid. Head moderately large; cranium transversely subelliptical in anterior view. Head hairs few and short; 2- to 5-branched. Labrum bilobed. Mandibles with the distal fourth long, slender, sharp-pointed and bent medially; mesal border erose. Galea a frustum, not finger-like.

The larvae of this genus have a dolichoderine habitus, resembling especially the larvae of *Dorymyrmex*.

Brachymyrmex depilis Emery

(Pl. II, figs. 10–15)

Stout and rather short; thorax curved ventrally to form an extremely short, stout neck; abdomen straight; posterior end narrowly rounded; diameter greatest at the third abdominal somite, diminishing gradually toward either end. Anus subterminal. Segmentation indistinct on the posterior half. Body hairs sparse and short; mostly 3- to 5-branched and 0.035–0.054 mm. long; on the dorsum of the abdomen a few are longer (about 0.07 mm.), whip-like and either simple or two-branched; no alveolus or articular membrane. Head moderately large; cranium transversely subelliptical; a fourth broader than long; gula with short transverse rows of spinules. Head hairs few, short (about 0.045 mm.), 2- to 5-branched; with alveolus and articular membrane. Each antenna with three sensilla. Labrum twice as broad as long, narrowed ventrally; bilobed due to a median impression of the ventral border; anterior surface with four small simple slender hairs and with four sensilla near the ventral border; posterior surface spinulose, the spinules minute and arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; about three large and three minute sensilla on the posterior surface of each lobe. Mandibles moderately sclerotized; wedge-shaped, with the edge medial; distal fourth bent medially to form a long slender, smooth, sharp-pointed apical tooth; basal three-fourths broadly subtriangular, with the mesal border erose and with anterior and posterior surfaces roughened with longitudinal and oblique ridges. Maxillae lobose; a few short longitudinal rows of spinules near the galea; palp a short frustum bearing two apical, two subapical and one lateral sensilla; galea a longer frustum, bearing two apical sensilla. Anterior surface of labium with a transverse band of spinules which are isolated or in short rows; palp a small frustum bearing two apical and two lateral sensilla; opening of sericteries a short transverse shelf projecting from the anterior surface. Hypopharynx spinulose, the spinules minute and arranged in subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: three larvae and 11 semipupae from New Jersey.)

Tribe **Gesomyrmicini** Wheeler

Genus **Gesomyrmex** Mayr

Thorax and first abdominal somite forming a short and very thick neck which is strongly arched ventrally; rest of abdomen somewhat swollen, straight and subcylindrical. Posterior end round. Body hairs sparse, simple and exceedingly minute. Head rather small; cranium transversely subelliptical in anterior view; integument sparsely spinulose. Antennae very small; each with two sensilla. Head hairs moderately numerous, simple and very short. Labrum small, feebly bilobed; posterior surface with six large sensilla near the center, around which are clustered 12 smaller sensilla. Mandibles heavily sclerotized; mesal border scalloped; distal fourth narrowed abruptly to form a slender, round-pointed apical tooth which is slightly curved medially. Maxillae with the apex round-pointed. Labial palp a low elevation bearing five sensilla.

Gesomyrmex kalshoveni Wheeler

(Pl. II, figs. 7–9)

Thorax and first abdominal somite forming a short and very thick neck which is strongly arched ventrally; rest of abdomen somewhat swollen, straight and subcylindrical. Lateral longitudinal welts feebly developed. Posterior end rounded. Leg, wing and gonopod vestiges present. Thirteen differentiated somites. Integument spinulose, the spinules minute and arranged in long transverse rows. Body uniformly and sparsely clothed with simple acuminate hairs, which are exceedingly minute (length 0.027–0.036 mm.); straight or slightly curved; alveolus and articular membrane present. Head rather small; cranium transversely subelliptical in anterior view, a third broader than long; integument sparsely spinulose, the spinules minute and in short transverse rows. Head hairs moderately numerous, simple, straight or slightly curved; acuminate; very short (length 0.027–0.036 mm.); alveolus and articular membrane present. Antennae very small; with two sensilla each. Labrum small; twice as broad (at base) as long; narrowed ventrally; bilobed due to a median incision of the ventral border; anteri-

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EXPLANATION OF PLATE II

Myrmelachista (*Decamera*) *zeledoni* Emery, Figs. 1–6. 1, head in anterior view, ×67; 2, left antenna in anterior view, ×867; 3, larva in side view, ×16; 4, two body hairs, ×185; 5, left mandible in anterior view, ×185; 6, left maxillary palp in anterior view, ×867.

Gesomyrmex kalshoveni Wheeler, Figs. 7–9. 7, head in anterior view, ×57; 8, body, hair, ×235; 9, left mandible in anterior view, ×121.

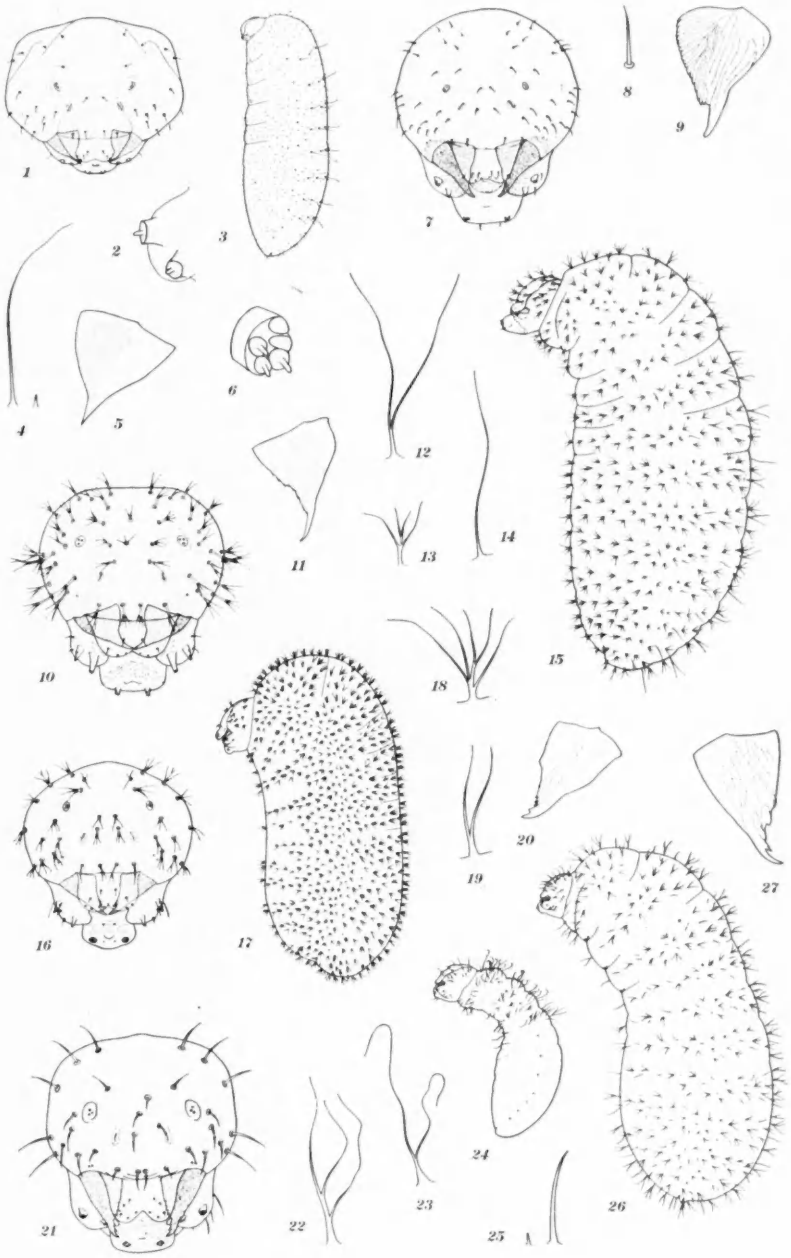
Brachymyrmex depilis Emery, Figs. 10–15. 10, head in anterior view, ×121; 11, left mandible in anterior view, ×235; 12–14, three body hairs, ×235; 15, larva in side view, ×44.

Paratrechina (*Nylanderia*) *melanderi* Wheeler, Figs. 16–20. 16, head in anterior view, ×95; 17, larva in side view, ×28; 18 and 19, two body hairs, ×333; 20, left mandible in anterior view, ×185.

Prenolepis imparis (Say), Figs. 21–27. 21, head in anterior view, ×86; 22 and 23, two branched body hairs, ×185; 24, very young larva in side view, ×22; 25, two simple body hairs, ×185; 26, larva in side view, × 22.

Larvae of Formicinae
Wheeler and Wheeler

PLATE II



or surface of each lobe with two hairs and (near the ventral border) three sensilla and with minute spinules which are isolated or in short rows; posterior surface sparsely spinulose, the spinules minute and arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally, posterior surface with about six large sensilla near the center, around which are 12 smaller sensilla. Mandibles heavily sclerotized; subtriangular in anterior view; wedge-shaped, with the edge medial; mesal border scalloped; distal fourth narrowed abruptly to form a smooth slender round-pointed apical tooth, which is slightly curved medially; basal three-fourths of anterior and posterior surfaces roughened with numerous longitudinal ridges. Maxillae with the apex paraboloidal, directed ventromedially and beset with spinules in short rows; palp a skewed peg, with one apical and 2 to 4 lateral sensilla; galea finger-like, with two apical sensilla. Labial palp a low elevation, bearing five sensilla; opening of sericteries a short transverse slit on the anterior surface of the labium. Hypopharynx with exceedingly minute spinules in rows which are grouped in two subtriangles whose bases are near the middle. (Material studied: two damaged integuments from Java.)

Wheeler, 1929*a*, p. 8:—The milk-white larvae "resemble those of other Formicinae in shape but are almost hairless. The head is very small and subglobular, the mandibles minute, with only an apical tooth which is drawn out into a slender, acute point. The semipupa measures a little over 7 mm. and is not enclosed in a cocoon."

Tribe **Prenolepidini** Forel

Plump and chunky; no neck; anterior end round. Segmentation indistinct. Head hairs few and short.

Genus **Prenolepis** Mayr

Plump and chunky; slightly curved ventrally; diameter nearly uniform but constricted at the first abdominal somite; ends rounded; not attenuated toward either end: head anteroventral; no neck. Anus terminal, with a small anterior and a conspicuous posterior lip. Thoracic somites feebly differentiated; abdominal somites indistinct. Body hairs sparse and short; of two types: (1) simple and (2) 2- to 3-branched. Cranium subheptagonal in anterior view. Head hairs few, short and simple. Mandibles with a slender short sharp-pointed medially curved apical tooth and one small subapical tooth; mesal border erose. Maxillae swollen ventrolaterally; apex narrowed to a conoid and directed medially; palp a small frustum; galea a frustum, not finger-shaped. Labial palp a small low knob.

The larvae of this genus have a distinctly dolichoderine habitus, resembling especially the larvae of *Dolichoderus*.

Prenolepis imparis (Say)

(Pl. II, figs. 21–27)

Plump and chunky; slightly curved ventrally; diameter nearly uniform but somewhat constricted at the first abdominal somite; ends rounded; not attenuated toward either end; prothorax with a low ventrolateral boss. Head anteroventral; no neck. Anus terminal with a

small anterior and a conspicuous posterior lip. Leg, wing and gonopod vestiges present. Thoracic somites feebly differentiated; abdominal somites indistinct. Posterodorsal surface of abdomen spinulose, the spinules minute and in short transverse rows. Body sparsely but uniformly furnished with short hairs of two types: (1) simple, 0.01–0.07 mm. long; (2) 2- to 3-branched, 0.04–0.09 mm. long, with the branches long and flexuous; no alveolus or articular membrane. Cranium subheptagonal in anterior view, a third broader than long; gula with short transverse rows of minute spinules. Hairs of head few, simple, slightly curved, short (0.05–0.07 mm.); with alveolus and articular membrane. Antennae with three sensilla each. Labrum bilobed due to a wide, deep incision of the ventral border; breadth (at base) nearly twice the length; narrowed ventrally; anterior surface of each lobe with three minute hairs and (near the ventral border) two sensilla; posterior surface densely spinulose, the spinules minute and arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; posterior surface with six sensilla near the middle. Mandibles moderately sclerotized; subtriangular in anterior view; wedge-shaped, with the edge medial; apical tooth smooth, short, slender, sharp-pointed and curved medially; one small, acute subapical tooth; mesal border erose; anterior and posterior surfaces roughened with a few longitudinal ridges. Maxillae swollen ventrolaterally; apex narrowed to a conoid and directed medially; palp a small frustum bearing four apical and one lateral sensilla; galea a small frustum bearing two apical sensilla. Labium with the anterior and lateral surfaces roughened with short transverse rows of minute spinules; palp a very small low knob bearing four sensilla. Opening of sericteries a short transverse slit on the anterior surface of the labium. Hypopharynx densely spinulose, spinules minute and arranged in numerous subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: numerous larvae from Ohio, courtesy of Dr. Mary Talbot.)

The very young larva is less plump. It has the four anterior somites distinct, bent ventrally and furnished with hairs. The rest of the abdomen is a little stouter and its segmentation is indistinct; it is somewhat attenuated toward the posterior end, which is round-pointed. The anus is ventral. The posterior half of body is destitute of hairs but spinulose.

The queen larvae are very similar to worker larvae except that the body is much larger and the head relatively smaller. (Material studied: two specimens from Illinois.)

Talbot, 1943:—"All brood was matured at about the same rate. . . . Larvae reached their height of abundance during the latter part of July and diminished during early August" in Ohio (p. 32). The egg-larval development required about 31 days; the pupal period was of the same length (p. 44). It is inferred that the larvae are fed by the repletes (p. 32).

Genus **Paratrechina** Motschoulsky

Plump, chunky and turgid; subellipsoidal; anterior end broadly rounded, posterior end round-pointed; no neck. Anterior end formed

from the dorsa of prothorax and mesothorax. Head ventral near the anterior end. Anus posteroventral. Segmentation indistinct. Body hairs moderately numerous and very short; 2- to 5-branched, the branches long, slender and flexible. Head large; cranium transversely subelliptical. Antennae very small. Head hairs few, short, of two types: (1) simple and (2) 2- to 6-branched. Mandibles small; with a blunt apical tooth and one small subapical tooth; surface ridges few. Maxillae with the apex paraboloidal. Labial palp a low elevation.

The larvae of this genus are decidedly dolichoderine in body shape, resembling especially the mature larvae of *Tapinoma:* the mouth parts, however, are formicine.

Paratrechina (Nylanderia) melanderi Wheeler

(Pl. II, figs. 16–20)

Plump, chunky and turgid; subellipsoidal; anterior end broadly rounded, posterior end round-pointed; no neck. Anterior end formed from the dorsa of prothorax and mesothorax. Head ventral, near the anterior end. Anus posteroventral. Segmentation indistinct. Leg vestiges present. Hairs moderately numerous and uniformly distributed; very short (about 0.036 mm.); 2- to 5-branched, the branches long, slender and flexible; no alveolus or articular membrane. Head large; cranium transversely subelliptical in anterior view; breadth 1.5x length. Head hairs few, short (about 0.036 mm.); simple or 2- to 6-branched: alveolus and articular membrane present. Antennae very small, each with three sensilla. Labrum bilobed due to a median impression of the ventral border; breadth 1.5x length: lateral borders sinuate: anterior surface with four minute hairs and with three sensilla near the ventral border of each lobe; posterior surface spinulose, the spinules minute and arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally: posterior surface with two groups of three sensilla each near the middle. Mandibles small: moderately sclerotized; subtriangular in anterior view; wedge-shaped, with the edge medial; with a small smooth apical tooth and one small subapical tooth, both blunt and directed medially; dorsal to these teeth the mesal border bears three to four acute denticles anterior and posterior surfaces with a few longitudinal ridges. Maxillae with the apex paraboloidal; palp a skewed peg bearing one subapical and three lateral sensilla; galea digitiform bearing two apical sensilla. Labium with a few transverse rows of minute spinules on the anterior surface: palp a low elevation bearing five sensilla; opening of sericteries a curved slit on the anterior surface of the labium. Hypopharynx spinulose, the spinules arranged in subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: 12 larvae from Oklahoma.)

The larvae of this genus are remarkable in that they differ greatly from other formicines but resemble very closely the larvae of the subfamily Dolichoderinae. The description, in fact, would almost fit the larva of *Dorymyrmex*. About the only non-dolichoderine character is the presence of branched hairs.

Paratrechina (Nylanderia) steinheili Forel

Eidmann, 1936, p. 99:—"Die Larven sind mit einem dichten und langen Pelz verzweigter Haare bedeckt."

Tribe **Formicini** Forel

Moderately stout; thorax and first abdominal somite forming a short stout neck which is curved ventrally; rest of abdomen straight; diameter greatest at the fourth abdominal somite, diminishing gradually toward either end. Body hairs short and moderately numerous. Mandibles robust; with the apical tooth sharply marked off from the rest, slender, smooth, round-pointed and slightly curved medially; mesal border denticulate near the base of the apical tooth. Maxillae swollen ventrolaterally; apex conoidal or paraboloidal and directed medially; opening of sericteries wide and salient, with two projections.

Genus **Pseudolasius** Emery

Pseudolasius myersi occipitalis Weber and Anderson

Weber and Anderson, 1950:—"Larva slender, hairs generally compound, mostly multifid, the longest in a 1.5-mm. larva about 0.03 mm. The larvae are white or slightly brownish with an easily observable dark intestinal mass about the level of the fifth to ninth segments. They are covered with bristly hairs which are best seen in the middle of the segments rather than in the trough of the segmental constrictions. These hairs, on examination under oil immersion, at a magnification of about 900 times, are seen to consist of a basilar scale or articulation socket and a branched stalk. The stalk divisions seem to be primarily of two types, one in which the stalk is thin and branches at the top only, the other in which the stalk is thicker and branches irregularly from shortly above the basal scale to the apex, the latter being divided into several branches" (p. 3). Figs. 8 and 9, hairs; fig. 16, larva in side view.

Genus **Lasius** Fabricius

Anus with anterior and posterior lips, the latter the larger. Five types of body hairs occur: (1) simple and slightly curved; (2) simple, long and whip-like; (3) denticulate; (4) 2- to 6-branched; (5) flat and many-branched, with the branches all in one plane. A larva is usually furnished with two or three of these types. Antennae small. Head hairs few and moderately long. Three types of head hairs occur: (1) simple, (2) denticulate and (3) 2- to 3-branched; a larva usually has two of these types. Mandibles subtriangular in anterior view; width (at base) about two-thirds the length; mesal border strongly convex and bearing a few denticles on the distal half; lateral border feebly convex.

Adlerz (1886) stated that the hairs of *Lasius* were similar to those of *Camponotus*, although of somewhat different form (p. 51). The body is flattened and its anterior third is strongly curved ventrally (p. 52). Brief reference to central nervous system (p. 58). "The larvae have branched, closely set hairs on the dorsal surface as well as the ventral.

The hairs are of the same type as those of *Camponotus* larvae, with sparse, long, fine-pointed branches or shorter and crowded branches. Woolly hairs . . . with fine, drawn-out tips, seldom with hook-like ends, as in *Camponotus*. In full-grown larvae I have found few bristles with lateral spines but on the other hand no woolly hairs or branched hairs" (p. 278; translated from the Swedish by Professor Edith E. Larson.)

Bischoff, 1927, p. 384:—The larvae of Lasius occasionally take solid food.

Donisthorpe, 1927*a*:—"The larvae practically occur in the nests throughout the year, being always present in the winter, and they take considerably longer to develop than is the case with the larvae of *Formica*. The workers feed the larvae with liquid food, but will also give them bits of dead insects, eggs, and other larvae, etc., to eat." (p. 207 = 1915, pp. 185–186). "Pale yellowish white, long, very narrow, and curved anteriorly, with the segments distinctly defined, and gradually increasing in breadth till just before the base. The whole body covered with short, slightly curved, yellow hairs of about equal length, which are more abundant in the younger larvae. The body appears to be finely striate transversely" (p. 210 = 1915, p. 187).

Donisthorpe, 1927*b*, p. 72:—Both adults and larvae of the staphylinid beetles, *Lamprinus* spp., devour eggs, larvae and pupae of *Lasius*.

Emery (1925, p. 227), referring to mermithogynes of *Lasius*: "Cette anomalie est due à un parasite du genre *Mermis*, qui se développe dans la larve et est contenu dans le gastre de l'imago."

Forel (1874) characterized the larvae of *Lasius* as "très mobiles" (p. 388 = 1920, p. 266) and stated that they grow very slowly (p. 389 = 1920, p. 267).

Gantes (1949, p. 88) asserted that the larvae of *Lasius*, *Formica*, and Cataglyphis are the most primitive of the Formicinae. "Larve néonate nue ou presque, mandibule bein développée et très coupante, poils de la larve adult très serrés. Larves agiles."

Gösswald (1934/5, p. 120) has given a general account of *Mermis* parasitism of this genus.

Janet, 1904, p. 33:—"Les jeunes larves de Lasius . . . sont couvertes d'un grand nombre de poils longs très fins et flexibles qui produisent un résultat analogue en s'enchevêtrant les uns dans les autres."

Wheeler, 1910, p. 405:—The clavigerid beetle *Claviger testaceus* often eats the larvae of *Lasius* spp.

Wheeler, 1928*a*, p. 202 (= 1926, p. 243):—The larvae may be given crude pieces of insects but the very youngest larvae (and possibly the older queen larvae) are fed regurgitated food.

Wheeler, 1933*a*, p. 10:—The colony-founding queen of *Lasius* may eat some of her own eggs, larvae and pupae.

The specific descriptions which follow are based upon material preserved in alcohol. The body shape of living larvae, especially when immature, may be somewhat different. The neck may be strongly curved (Pl. III, figs. 27 and 28) so that the head is directed posteriorly; the lateral longitudinal welts may be narrow, thick and conspicuous.

Also we suspect that the proportions and distribution of the several types of hairs will vary from instar to instar in the same individual. To verify this, however, would require a study in itself and we have not attempted it.

Subgenus **Lasius** Fabricius

Cranium suboctagonal in anterior view. Maxillae apparently without spinules; palp a skewed peg. Labial palp a frustum.

Lasius alienus americanus Emery

(Pl. III, figs. 1–8)

Moderately stout; thoracic and first abdominal somites forming a short stout neck which is slightly curved ventrally; rest of abdomen elongate-subellipsoidal; posterior end broadly rounded. Lateral longitudinal welts feebly developed. Anus terminal with anterior and posterior lips, the latter being the larger. Ten differentiated somites. Body hairs mostly short, moderately abundant and uniformly distributed, except on large intersegmental areas which are naked; without alveolus and articular membrane. Hairs of three types: (1) denticulate, 0.07–0.18 mm. long; (2) 2- to 3-branched (rarely 4), 0.05–0.07 mm.long; (3) long (about 0.13 mm.) and whip-like; branched hairs predominate (ratio 5:1) on dorsal and lateral surfaces. Cranium suboctagonal in anterior view; a third broader than long. Head hairs few, moderately long (0.05–0.07 mm.), denticulate or 2- to 3-branched; with alveolus and articular membrane. Antennae very small with two or three sensilla. Labrum bilobed due to a wide incision of the ventral border; slightly narrowed ventrally; breadth (at base) nearly twice the length; anterior surface of each lobe with three or four short hairs and about six sensilla on or near the ventral border; posterior surface densely spinulose, the spinules minute and arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; about 12 sensilla near the middle of the posterior surface. Mandibles robust and moderately sclerotized; wedge-shaped, with the edge medial; apical tooth sharply defined, slender, smooth, round-pointed and slightly curved medially and posteriorly; mesal border strongly convex and bearing a few denticles near the base of the apical tooth; lateral border feebly convex; anterior and posterior surfaces roughened by numerous longitudinal ridges. Maxillae swollen ventrolaterally; apex conoidal and directed medially; palp a skewed peg bearing one apical, two subapical and one lateral sensilla; galea a rather slender cone bearing two apical sensilla. Anterior surface of labium with a few minute spinules in short arcuate transverse rows; palp a frustrum bearing one apical, two subapical and two lateral sensilla; opening of sericteries a wide shelf on the anterior surface. Hypopharynx densely spinulose, the spinules arranged in subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: numerous larvae from North Dakota.)

Sexual larvae are similar to worker larvae except that the body is larger and plumper while the head is relatively smaller; male larvae are intermediate between those of queens and workers.

The following notes were taken by the senior author while observing

living *americanus* larvae in 1920:—Five larvae are apparently sucking out the juices of a somewhat shriveled dead larva (same brood). The heads move rhythmically back and forth like pumps. One larva stops pumping, ejects a quantity of clear fluid from the mouth onto the carcass, rests with its mouth near the carcass and in the bubble of liquid, then sucks in the liquid and resumes pumping operations. The mandibles move from side to side during the pumping procedure. The mouth, or a part of it, is in the form of a short suckerlike proboscis which is worked back and forth in the pumping. Occasionally a larva stops, withdraws its head and licks its chops (apparently). When the carcass is lifted away with forceps the larvae adhere to it rather firmly.

Forbes, 1908:—"The workers feed their larvae almost constantly from the contents of their own stomachs, and often mouth and hover them, a mass of the ants clustering around and over them in a way to conceal them from view" (pp. 39–40). One of the figures on Plate I (p. 45) is an excellent wash drawing of a larva in side view (repeated: Sanderson, 1912, Fig. 123 on p. 168; Sanderson and Peairs, 1921, Fig. 130 on p. 154; Wellhouse, Fig. 155 on p. 343).

Tanquary, 1913:—The life cycle was reported as: egg 23–48 days, larva 16–39 days, pupa 20–40 days; averages 34, 26.4 and 27.1 respectively (pp. 425–434). "The length of the different stages varies with conditions. The larval stage may extend over more than a year. . . . During the winter, nests of this species contain only dealated females, workers, and larvae. . . . A small percentage of the pupae of this ant are naked, some of them owing to a failure of the larvae to attach their first silken threads. . . . The workers will eat some of the larvae, even though plenty of food is provided" (p. 441).

Wellhouse, 1926:—"The larvae are white, maggot-like creatures, curved at the smaller end, where a small but distinct head and a pair of jaws are located. The body bears a thin covering of hairs for protection" (p. 340). Fig. 155 on page 343, repeats Forbes (1908).

Lasius alienus (Förster)

Eidmann (1943, p. 236) found larvae in an overwintering colony.

Stärcke (1939, p. XIX and Figs. 1 and 2 on p. XX) has discussed internal anatomy of the antennae.

Wheeler (1928*a*, p. 205=1926, p. 248; and 1928*b*, p. 170) has discussed mermithogynes of this species; presumably the nematode larvae had parasitized the ants in the larval stage.

Lasius brunneus (Latreille)

Donisthorpe (1927*b*) discovered that a pselaphid beetle (*Batrisodes delaportei* Aub.) ate the brood of this ant (p. 45) and suspected that a staphylinid beetle (*Euryusa sinuata* Er.) did likewise (p. 72). He also reported that Silvestri found that another staphylinid (*Homoeusa acuminata* Kr.) devoured the larvae of this ant (p. 29).

Lasius niger (Linnaeus)

Adlerz (1886, p. 150) saw seven larvae of this ant arranged in a circle with their heads toward the center and their mouth buried in a

little ant larva. The larvae are often found sucking out smaller dead ants of other species.

Berlese (1909, Fig. 905 on p. 729) has illustrated a sagittal section of the pyloric region of the alimentary canal.

Donisthorpe, 1915, Pl. III = 1927*a*, Pl. III:—A photograph of a larva in side view.

Donisthorpe (1927*b*, p. 97) mentioned the probability that a mymarid wasp (*Litus cynipseus* Hal.) "had bred out from the eggs of the ants."

Eidmann, 1928*b*, p. 40:—"Die dichte Behaarung der überwinterten Larven kommt daher, dass der Körper der Larven durch die Entbehrungen der Überwinterung stark schrumpft und die Behaarung daher dichter erscheint als bei gut genährten Tieren."

Eidmann (1943, pp. 233–236) stated that the overwintering colony might or might not include larvae.

Gantes, 1949:—"La larve est beaucoup plus petite: 3 mm. Le corps est couvert de poils plus serrés, de plusieurs types: 1. *Poil simple*, long, fin, très souple, de 0 mm. 18. Se trouve surtout sur le bout de l'abdomen. 2. *Poil épineux* couvert d'épines sur la moitié supérieure, droit, mesurant 0 mm. 09; le tronc principal peut se diviser en deux branches secondaires également épineuses. On les trouve sur tout le corps, mais particulièrement sur le thorax. 3. *Poil épineux* beaucoup plus court et sur toute sa hauteur. 4. *Poil bifurqué* au tiers de sa hauteur. Il débute par un tronc large et épais qui se divise en deux branches devenant de plus en plus fines. Ils ont 0 mm. 10 de long. Les mandibules sont bien différenciées d'un brun très clair; elles ont la même forme que celles de *Formica:* elles mesurent 0 mm. 119" (p. 77). Fig. II on Pl. II: hair of mature larva, hair of young larva and mandible. "La jeune larve a simplement le corps couvert de poils longs et fins qui s'enchevêtrent les uns dans l'autre; ces poils se trouvent sur tout le corps, puis on les voit régresser sur le bout de l'abdomen pendant que les poils bifurqués définitifs apparaissent sur le corps" (p. 87). Growth is treated briefly on pages 85 and 86.

Goetsch (1937, p. 137) gave the life cycle of the *Gartenameise* (presumably *L. niger*) as: egg 13–30 days, larva 9–24 days, pupa 16–36 days.

Janet, 1897, pp. 10–11:—"Sur un petit Ver de terre . . . il y avait une vingtaine de larves qui paraissaient occupées à le sucer. Les larves restèrent quelque temps attachées à ce Ver que j'enlevai tout doucement, mais bientôt je les vis toutes, successivement, lacher prise et retomber par terre."

Leeuwenhoek (1719, Figs. 5 and 6):—A larva in side view, probably *L. niger*.

Mayr, 1855, p. 283:—"Sie sind im Frühjahre oder im Beginne des Sommers in den Colonien anzutreffen, doch erzählt Gould, dass er auch Larven der *Formica nigra* und *Form. flava* im Winter am Grunde des Baues fand, und fügt noch die interessante Notiz hinzu, dass diese Larven viel dichter behaart waren, als jene, welche im Sommer gefunden werden."

Wheeler (1928*a*, p. 205 = 1926, p. 248) discussed mermithogynes of this species: presumably the nematode larvae had parasitized the ants in the larval stage.

Lasius niger neoniger Emery

"Dr. N. A. Cobb, our well-known authority on the nematodes, . . . writes me that he has found the larva of *Allomermis myrmecophila* Bayliss—'in the body cavity of a queen grub of . . . *neoniger*'" (Wheeler, 1930, p. 53). (See also Wheeler, 1928*a*, p. 205 = 1926, p. 248; and 1928*b*, p. 170.)

Lasius schiefferdeckeri Mayr

Wheeler (1914, p. 121) referred to a block of Baltic amber containing a larva of this extinct species.

Subgenus **Chthonolasius** Ruzsky

Cranium transversely subelliptical in anterior view. Anterior surface of labrum with denticulate hairs and with a median longitudinal furrow. Mesal surface of maxillae spinulose; palp a skewed thick-based peg. Labial palp a low knob.

Lasius (Chthonolasius) umbratus aphidicola (Walsh)

(Pl. III, figs. 9–16)

Moderately stout; thorax and first abdominal somite forming a short stout neck which is slightly curved ventrally; rest of abdomen elongate-subellipsoidal; lateral longitudinal welts broad and low. Posterior end rounded. Anus subterminal with anterior and posterior lips, the latter being the larger. Leg, wing and gonopod vestiges present. Thirteen differentiated somites. Body hairs mostly short, rather sparse and uniformly distributed, except on large intersegmental areas which are naked; without alveolus and articular membrane. Hairs of three types: (1) simple, slender, whip-like, 0.036–0.13 mm. long, the most abundant type; (2) stout, 0.06–0.12 mm. long and denticulate with numerous fine short branches; (3) 2- to 3-branched, 0.054–0.12 mm. long, the least abundant type. Cranium transversely subelliptical in anterior view; slightly broader than long; with a slight genal bulge. Head hairs few, rather short (0.05–0.07 mm.), denticulate, with alveolus and articular membrane. Antennae very small with three (sometimes two) sensilla. Labrum bilobed due to an incision of the ventral border; breadth (at base) nearly twice the length, slightly narrowed ventrally; anterior surface with a median longitudinal furrow, with two or three short denticulate hairs on each lobe and with two or three sensilla on or near the ventral border of each lobe. Posterior surface of labrum spinulose, the spinules minute and arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; about six large sensilla near the middle and about five small sensilla near the center of each lobe. Mandibles robust and moderately sclerotized; wedge-shaped, with the edge medial; apical tooth sharply defined, slender, smooth, round-pointed and slightly curved medially; mesal border strongly convex and bearing a few denticles on the distal half; lateral border feebly convex; anterior and posterior surfaces roughened with numerous longitudinal ridges. Maxillae slightly swollen ventrolaterally; apex paraboloidal and directed medially; mesal surface furnished with minute spinules arranged in numerous

short arcuate rows; palp a skewed peg with a stout base, bearing one apical, three subapical and one lateral sensilla; galea finger-like, with two apical sensilla. Anterior surface of labium with short curved mostly transverse rows of spinules of various lengths; palp a low knob bearing five sensilla; opening of sericteries wide and salient with two projections. Hypopharynx densely spinulose, the spinules minute and arranged in subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: numerous larvae from North Dakota and Massachusetts.)

Observations on living larvae of various sizes:—They are capable of remarkable changes in shape. At one moment the body may be elongate and subcylindrical, with the neck slightly bent ventrally and with the segmentation indistinct. Upon stimulation it may change in a short time to a C-shaped creature with all segments distinct, with the venter depressed and, with the aid of the now conspicuous lateral longitudinal welts, forming a trough.

Park, 1932:—The clavigerid beetles *Adranes lecontei* Brendel embrace larvae of *aphidicola*, raking them with their tarsi, stroking them with their antennae, licking them and biting the surface. "The beetles, then, would appear to feed on the host larvae, at least in part, this food being composed of integumental exudates, oils, excretions, and possibly body fluid" (pp. 82–84). Fig. 2 on page 83 shows a beetle clasping an ant larva and licking its anterior somites. The pselaphid beetle *Ceophyllus monilis* Lec. was observed feeding on a dead ant larva (p. 87).

Park, 1947:—Clavigerid beetles of the genus *Adranes* occasionally scrape, puncture and suck eggs, larvae and pupae (p. 39). Fig. 5, p. 39 = Park, 1932, Fig. 2. The pselaphid beetle *Ceophyllus monilis* Lec. licks larvae and eats dead larvae (p. 40).

Lasius (Cthonolasius) umbratus meridionalis Bondroit

Wheeler (1928*a*, p. 205 = 1926, p. 248, and 1928*b*, p. 171) has discussed mermithogynes of this ant; presumably the nematode larvae had parasitized the ants in the larval stage.

Lasius (Chthonolasius) umbratus mixtus (Nylander)

Janet, 1897, p. 10:—"J'ai constaté, au moment de la capture . . . , qu'un certain nombre de grosses larves avaient, bien exactement devant la bouche, de petites masses molles qu'elles semblaient sucer. En examinant, à la loupe, quelques-unes de ces larves mises à part dans un nid artificiel, j'ai constaté des mouvements buccaux bien nets. Il est à peu près certain que ces larves aspiraient la partie liquide de ces petites masses molles dont quelques-unes étaient les restes de larves semblables à celles qui les suçaint." (Referred to by Wheeler, 1933*a*, p. 15.)

Lasius (Chthonolasius) flavus nearcticus Wheeler

Similar to *aphidicola* except in the following details:—Body hairs more numerous and of only two types: (1) 0.06–0.12 mm. long, with 2 to 6 long slender branches, the more abundant type; (2) 0.11–0.14 mm. long, simple, very few. Cranium a third broader than long; genal

bulge more prominent. Head hairs moderately numerous and longer; mostly simple, rarely branched or denticulate; labium with the spinules isolated and larger. (Material studied: eight larvae from New York.)

Lasius (Chthonolasius) flavus microps Wheeler

(Pl. III, figs. 17–21)

Similar to *nearcticus* except in the following characters:—Hairs of three types: (1) simple 0.04–0.11 mm. long; (2) 2- to 3-branched, 0.04–0.11 mm. long; (3) dendritic, flat, with stout base and numerous short slender branches which are all in the same plane, 0.04–0.06 mm. long. Head hairs shorter, of two types: (1) 2- to 3-branched; (2) denticulate. Apical tooth of mandible longer and more slender. (Material studied: numerous larvae from North Dakota.)

Lasius (Chthonolasius) flavus (Fabricius)

Adlerz (1886, pp. 52–53) discussed the apparent increase in hairiness of hibernating larvae. He stated (p. 52) that hairs of young larvae were approximately one-fifth of the body length.

De Geer, 1778, Pl. XIII, Fig. 26:—A larva in side view, probably *L. flavus*.

Donisthorpe (1927*b*) has seen the clavigerid beetle *Claviger testaceus* Preys. eat ant larvae (presumably *L. flavus*) (p. 14). The histerid beetle *Hetaerius ferrugineus* 01. "feeds on dead and wounded ants, and their larvae and pupae, mites, etc." (p. 51). "When examining a nest of *flavus* . . . I observed [a staphylined beetle, *Myrmedonia limbata* Pk.,] seizing one of the ant's larvae and dragging it out of the nest" (p. 67).

Eidmann (1943, pp. 236–243) concluded that *flavus* overwinters either with or without larvae.

Goetsch (1937, p. 137) gave for the life cycle: egg 22–52 days; larva 7–31 days, pupa 16–49 days.

Janet, 1897, p. 11:—"Dans un nid naturel de *Lasius flavus*, à un moment où les galeries superficielles étaient remplies de progéniture (13 août), j'ai vu deux groupes, de chacun cinq grosses larves, qui légèrement recourbées sur elles-mêmes, et plus ou moins enchevêtrées les unes dans les autres, avaient, toutes les cinq dans chaque groupe, la bouche appliquée et comme collée sur une petite masse de substance molle et gluante. Dans un nid artificiel, de la même espèce, j'ai observé

EXPLANATION OF PLATE III

Lasius alienus americanus Emery, Figs. 1–8. 1, head in anterior view, ×86; 2, right mandible in anterior view, ×185; 3–7, five body hairs, ×185; 8, larva in side view, ×20.

Lasius (Chthonolasius) umbratus aphidicola (Walsh), Figs. 9–16. 9, head in anterior view, ×76; 10, right mandible in anterior view, ×185; 11, head and thorax in ventral view to show leg vestiges, ×28; 12–16, five body hairs, ×185.

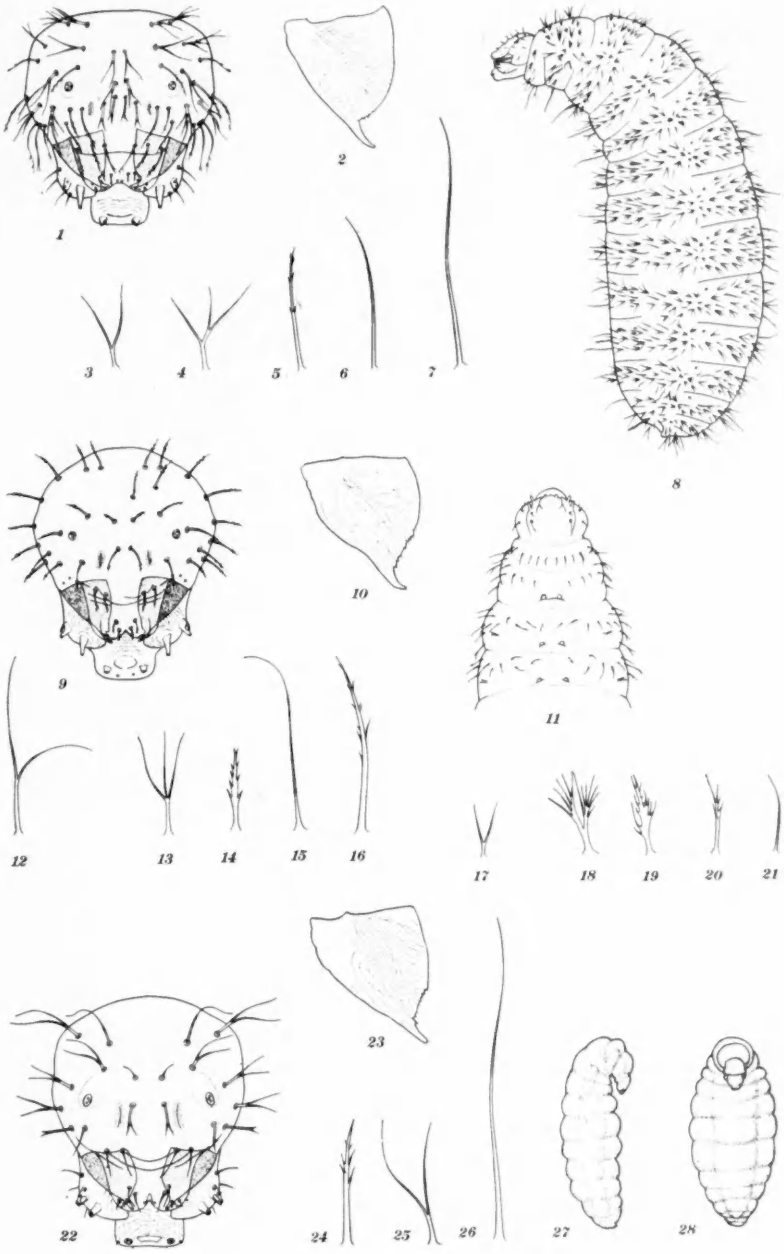
Lasius (Chthonolasius) flavus microps Wheeler, Figs. 17–21, five body hairs, ×185.

Lasius (Acanthomyops) subglaber Emery, Figs. 22–26. 22, head in anterior view, ×86; 23, right mandible in anterior view, ×185; 24–26, three body hairs, ×185.

Lasius (Acanthomyops) claviger (Roger), Figs. 27 and 28. 27, ♀ larva in side view (hairs omitted), ×7; 28, ♀ larva in ventral view (hairs omitted), ×7.

Larvae of Formicinae
Wheeler and Wheeler

PLATE III



(fig. 3) un groupe de trois grosses larves occupées à sucer une masse molle, allongée, qui s'est flétrie de plus en plus sous mes yeux. En examinant la cuticule chitineuse du résidu j'ai pu vérifier que la victime, qui avait servi de repas aux trois grosses larves, n'était autre qu' une de leurs semblables." (Referred to by Wheeler and Bailey, 1920, p. 251.)

Janet, 1904, p. 33:—"Dans un nid artificiel, des Lasius flavus avaient entassé des milliers de très jeunes larves au point de remplir, sur plusieurs centimètres de longueur, une vaste chambre de forme allongée. Ces petites larves étaient liaisonnées par leurs poils les unes avec les autres. Les Fourmis avaient pu, simplement en enlevant, après coup, un certain nombre de ces larves, creuser dans cette masse vivante, de véritables galeries, de 2 millimètres de diamètre, juste suffisantes pour le passage d'une ouvrière."

Karawaiew, 1898, p. 402:—"Die junge milchweisse Larve von Lasius ist madenförmig, mit einem zugespitzten Vorderende und etwas gegen das Hinterende verdicktem Körper. Bei fixirten Larven ist das Hinterende ein wenig, das Vorder- resp. Kopfende stark gegen die Bauchseite gekrümmt, so dass die Form des Medianschnittes sehr der Klinge eines Gartenmessers gleicht. Der Kopfabschnitt ist vom ersten Brustsegmente ziemlich scharf durch eine Ringfalte abgegrenzt und trägt zwei Paar kurzer chitinbewaffneter Mundwerkzeuge (Mandibeln und Maxillen); von oben und von unten wird die Mundöffnung von je einer Lippe bedeckt. Die Zahl der Segmente, den Kopfabschnitt für ein einziges Segment gerechnet, ist 14, die Zahl der Abdominalsegmente also 10." Fig. 11 shows the sericteries in a profile outline of a larva (repeated: Wheeler, 1910, Fig. 124B on p. 222 and Karawaiew, 1906).

Karawaiew, 1900:—Internal metamorphosis.

Karawaiew, 1906, Fig. 11:—Profile of larva enclosing spinning glands. Referred to by Karawaiew, 1929, p. 252. Repeated by Wheeler, 1910, Fig. 124B on p. 222.

Lubbock, 1882, Pl. 5, fig. 3:—Larva in side view.

Mayr, 1855, p. 283:—See under *L. niger*.

Wheeler, 1910, p. 405:—The clavigerid beetle *Claviger testaceus* "is fed with regurgitated food, although it often eats the ant larvae."

Wheeler (1928*a*, p. 205=1926, p. 248; and 1928*b*, p. 170) has discussed mermithogynes of this species; presumably the nematode larvae had parasitized the ants in the larval stage.

Subgenus **Dendrolasius** Ruzsky

Lasius (**Dendrolasius**) **fuliginosus** (Latreille)

Adlerz (1886, p. 278):—"Woolhairs" are especially abundant in this species; the tips are usually finely attenuated, rarely hooked.

Eidmann (1943, pp. 228–233):—Larvae overwinter in the nest.

Subgenus **Acanthomyops** Mayr

Cranium subheptagonal in anterior view. Medial surface of maxillae spinulose; palp a skewed peg. Labial palp a low knob.

Wheeler & Bailey, 1920, p. 251:—The larvae of this subgenus have been observed to feed on whole insects or pieces of insects.

Lasius (Acanthomyops) subglaber Emery

(Pl. III, figs. 22–26)

Moderately stout; thoracic and first abdominal somites forming a short stout neck which is slightly curved ventrally, with the diameter decreasing anteriorly; rest of abdomen elongate-subellipsoidal. Posterior end rounded. Lateral longitudinal welts feebly developed. Anus terminal with anterior and posterior lips, the latter being the larger. Leg, wing and gonopod vestiges present. Body hairs mostly short, moderately numerous and uniformly distributed except on narrow intersegmental areas which are naked; without alveolus and articular membrane. Hairs of three types: (1) 2- to 3-branched, 0.05–0.1 mm. long; (2) denticulate, with stout base and several short branches, 0.05–0.11 mm. long; (3) a few simple flexuous hairs, 0.13–0.25 mm. long, longest on the ventral surface. Integument sparsely spinulose, spinules minute and in subtransverse rows. Cranium subheptagonal in anterior view, slightly broader than long, with a slight genal bulge. Head hairs few: moderately long (0.06–0.1 mm.): of two types, (1) simple and (2) 2- to 3-branched; with alveolus and articular membrane. Antennae small; each mounted on a low convexity and bearing three sensilla. Labrum bilobed due to a median incision of the ventral border; breadth (at base) nearly twice the length; slightly narrowed ventrally; anterior surface of each lobe with three or four short hairs and two or three sensilla; ventral border of each lobe with two sensilla; posterior surface densely spinulose, spinules minute and arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; six large and ten small sensilla on the posterior surface. Mandibles robust and moderately sclerotized; wedge-shaped, with the edge medial; subtriangular in anterior view; apical tooth sharply defined, slender, round-pointed, straight and directed medially; mesal border strongly convex and bearing a few denticles on the distal half; lateral border feebly convex; anterior and posterior surfaces roughened by numerous longitudinal ridges. Maxillae swollen ventrolaterally; apex paraboloidal and directed medially with a few minute spinules in short rows on the mesal surface; palp a skewed peg with two apical, two subapical and one lateral sensilla; galea digitiform with two apical sensilla. Labium with anterior surface sparsely spinose, the spinules minute and in short rows; palp a low knob bearing five sensilla; opening of sericteries a transverse shelf on the anterior surface of the labium. Hypopharynx densely spinulose, the spinules minute and arranged in subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: numerous larvae from North Dakota.)

A half-grown larva resembles the mature larva, except that the body is more slender and more conspicuously segmented and the head hair are all denticulate.

Lasius (Acanthomyops) claviger (Roger)

(Pl. III, figs. 27 and 28)

Similar to *subglaber* but differing as follows: Body hairs all denticulate. Head hairs shorter and all denticulate. (Material studied: four damaged specimens from New York and one from New Hampshire.)

Immature larvae are more slender and more conspicuously segmented.

Wheeler, 1933*a*, p. 15:—"The larvae are fed on pieces of insects captured by the workers, instead of with regurgitated liquid food."

Lasius (Acanthomyops) interjectus Mayr

Similar to ***subglaber*** except in the following details: Body hairs somewhat shorter; denticulate the least numerous. Head hairs all denticulate. Maxillary palp a skewed peg with one apical, one subapical and three lateral sensilla. (Material studied: numerous larvae from North Dakota.)

Immature larvae are more slender and more conspicuously segmented.

Genus **Myrmecocystus** Wesmael

Myrmecocystus melliger Forel

McCook, 1882:—"When the grub is to be cleansed it is taken in the mouth, turned by the fore pair of legs, the antennae meanwhile touching and apparently aiding, while the mandibles are applied over the grub, their teeth apparently working chiefly within the annular divisions of the several joints. Doubtless this motion is accompanied by a free use of the tongue, but this I did not observe. When the grubs are to be fed, the workers pass from one to another, striding over them, and standing among them as they lie in little groups. The wee white things perk up their brownish yellow heads, which they stretch out and move around, evidently soliciting food. Their nurses move from one to another, apply the mouth for a moment, and pass on" (p. 46). Pl. VI, Fig. 34, shows workers feeding larvae.

Genus **Cataglyphis** Förster

Cataglyphis albicans Roger

Gantes, 1949:—"Cette espèce est remarquable par la grosseur de ses larves. Une jeune larve mesure 3 mm. et à une forme spéciale: en poire. L'abdomen est gonflé et la tête fine: le corps se rétrécit à partir des segments thoraciques qui sont les seuls distincts. La larve est nue sauf quelques rares poils sur la tête. Les mandibules sont des triangles dont la base s'insère dans la tête et l'apex se termine par une pointe fine. La larve au 5e stade mesure 8 mm. de long et 2 mm. de large; le corps est massif, un peu en forme de massue. Il est arqué vers le 3e anneau thoracique, de sorte que la tête est repliée ventralement: cette incurvation est plus accentuée que chez *Formica*. La forme générale, le nombre de segments sont identiques à *Formica*. La tête, fine et mobile, permet aux larves de se nourrir seules: je les ai vu plonger la tête dans un abdomen d'insecte. Tout le corps est couvert de poils simples, denses, rigides, qui sont nettement rangés en quinconce vers le bout de l'abdomen; à cet endroit, ils sont plus longs, 0 mm. 18, puis ils se raccourcissent en se rapprochant de la tête: sur le thorax 0 mm. 13 et sous la tête 0 mm. 028. La tête ressemble à celle de *Formica*. Les mandibules sont très grandes, 0 mm. 19, mais

la larve est beaucoup plus grosse. Elles ont à peu près la même forme, mais sont d'un brun foncé et les parties s'insérant dans la tête sont plus épaisses" (pp. 76–77). Pl. II, fig. 1, shows a young larva, body hairs and a mandible. "Les larves sont nues jusqu'au stade III" (p. 87). Growth is discussed on pages 85, 86 and 87. The larva is primitive: "larve néonate nue ou presque, mandibule bien développée et très coupante, poils de la larve adulte très serrés. Larves agiles" (p. 88).

Cataglyphis bicolor (Fabricius)

Athias-Henriot (1947):—Internal anatomy, pp. 260, 263, and 264. "Carnivore" (p. 260).

Cataglyphis viatica (Fabricius)

Bedel (1895) collected *Eucharis bedeli* Cameron with "*Myrmecocystus viaticus*" in Algeria. The ant might be either this species or *C. bicolor*. Presumably the eucharid larva was parasitoid on the ant larva. (Referred to by Ruschka, 1924, p. 87.)

Cataglyphis (Machaeromyrma) bombycina Roger

La larve "a une tête petite, le corps couvert d'une fine pubescence et de grand macrochètes simples clairsemés. La cuticle est chagrinée (mais ceci est peut-être dû à la préparation). En dehors de la pubescence, il n'y a pas d'adaptation particulière à la vie dans le sable chez cette Fourmi saharienne" (Athias-Henriot, 1947, p. 252).

Bernard, 1948, p. 107:—Les larves sont "couvertes de poils courts, droits: loin de s'accrocher au sable, elles roulent sur lui quand on ouvre le terrier."

Genus **Formica** Linnaeus

Prothorax with a pair of lateral swellings. Anus with a prominent posterior lip. Body hairs mostly with bifid tips. Antennae large and drumlin-shaped (=semiovoidal). Head hairs moderately numerous, short, mostly with bifid tips. Labrum small; anterior surface of each lobe with ventrolateral swelling. Mandibles roughly quadrangular in anterior view; breadth (at base) nearly equal the length; mesal border convex; lateral border obtusely angulate near the middle. Maxillae with the apex spinulose; palp a skewed peg. Labial palp a low knob.

Adlerz, 1886:—"Larvae not flattened, posterior part of body greatly expanded. Dorsal as well as ventral surface clothed with a few short bristly hairs" (p. 283; translated from the Swedish by Professor Edith E. Larson). Internal anatomy—pages 58–64.

Bischoff, 1927, p. 384:—The larvae of this genus occasionally take solid food.

Buchsbaum, 1948, p. 292–25:—Photograph of ant brood, probably that of *Formica* sp.

Clausen, 1940, p. 221:—*Eucharis* is most frequently associated with *Formica:* the eucharid larvae are parasitic on the mature larvae or pupae of the ants.

Donisthorpe, 1927*a*:—"Pale yellowish white, long, narrow and curved anteriorly; head considerably narrower than the rest of the body;

segments well defined, transversely striate, and gradually increasing in width till just before the distal end. The whole body covered with short straight hairs of equal length, which appear to be bifid at the apex, and are more abundant on the younger larvae." (p. 284 = 1915, p. 243).

Donisthorpe, 1927*b*, p. 17:—Staphylinid beetles of the genus *Atemeles* eat the larvae of *Formica*.

Emery, 1899, p. 5:—The mandibles of ponerine larvae are much larger than those of the larvae of *Formica*.

Forel, 1874, p. 389 (=1920, p. 266):—Les larves "des *Formica* croissent vite."

Gantes, 1949:—"Les larves de *Formica* sont des larves assez primitives: tête mobile, à mandibules bien développées: ces larves se nourrissent seules; la tête est repliée sur la ventre, qui sert de table sur laquelle l' ♀ dépose la nourriture. Les jeunes larves sont à peu près nues" (p. 76). "Ont une très forte croissance aux stades IV et V, vingt fois plus intense. Ce type semble le cas des larves primitives: il se rapproche de celui des guêpes" (p. 85). "*Formica, Lasius, Cataglyphis* sont les plus primitifs: larve néonate nue ou presque, mandibule bien développée et très coupante, poils de la larve adulte très serrés. Larves agiles" (p. 88).

Herbert, 1934, p. 21:—Photograph of a larva, probably *Formica*.

Wheeler, 1910:—The larvae of the myrmecophilous staphylinids *Lomechusa*, *Atemeles* and *Xenodusa* feed on the larvae of *Formica*, pp. 406–7; also 1923*b*, p. 230 (=1923*a*, p. 30). The presence of *Lomechusa* within the *Formica* nest leads to the withholding of food from the ant larvae; the result is pseudogynes (p. 422). Wheeler also cited numerous papers by Wasmann on these beetles, which we have not consulted.

Subgenus **Proformica** Ruzsky

Cranium subrectangular in anterior view slightly broader than long with the corners rounded. Mandibles with the mesal border jagged near the base of the apical tooth.

Formica (Proformica) neogagates Emery

(Pl. IV, figs. 8–10)

Body stout; thorax and abdominal somite I strongly curved ventrally, rest of abdomen straight; diameter greatest at the fourth abdominal somite, diminishing gradually toward either end; posterior and narrowly rounded; lateral longitudinal welts feebly developed; prothorax with a pair of lateral swellings. Anus terminal, with a prominent posterior lip. Leg, wing and gonopod vestiges present. Thirteen differentiated somites. Body hairs moderately abundant; short (0.05–0.08 mm.); uniformly distributed; without alveolus and articular membrane. Hairs mostly with the tips bifid (rarely with the branches forked), very rarely with the tip unbranched. Integument spinulose, spinules minute and in transverse rows. Cranium subrectangular in anterior view, slightly broader than long with the corner rounded. Head hairs moderately numerous; short (0.05–0.08 mm.); mostly with bifid tips, a very few trifid or simple. Antennae large;

drumlin-shaped; with three sensilla each. Labrum small and short; breadth (at base) a little more than twice the length; narrowed ventrally; ventral corners rounded; bilobed due to a wide depression in the ventral border; anterior surface of each lobe with a ventrolateral swelling which bears two or three sensilla and two or three minute hairs; ventral border of each lobe with three sensilla; posterior surface spinulose, the spinules minute and arranged in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; posterior surface with about a dozen scattered sensilla. Mandibles rather small and moderately sclerotized; short and stout; breadth (at base) nearly equal to length; roughly quadrangular in anterior view; mesal border strongly convex; lateral border obtusely angulate near the middle; wedge-shaped, with the edge medial; apical tooth sharply defined, slender, smooth, tapering, round-pointed and slightly curved medially; mesal border jagged near the base of the apical tooth; anterior and posterior surfaces roughened with numerous sublongitudinal ridges. Maxillae swollen ventrolaterally; apex paraboloidal and directed medially; apex spinulose, the spinules minute and in short rows; palp a skewed peg, with one apical, two subapical and one lateral sensilla; galea finger-like, with two apical sensilla. Anterior and lateral surfaces of labium with short arcuate subtransverse rows of minute spinules; palp a low knob bearing four sensilla; opening of sericteries wide and salient, with two projections. Hypopharynx densely spinulose, the spinules minute and in numerous subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: numerous larvae from North Dakota.)

Young larvae similar to mature larvae except as follows: head relatively larger; anus ventral; integumentary spinules more conspicuous posteriorly; hairs sparser.

Subgenus **Neoformica** Wheeler

Cranium subcircular in anterior view. Mandibles with the mesal border denticulate near the base of the apical tooth.

Formica (**Neoformica**) **pallidefulva nitidiventris** Emery

(Pl. IV, figs. 15–17)

Body stout; thorax and abdominal somite I curved ventrally, rest of abdomen straight; diameter greatest at the fourth abdominal somite, diminishing gradually toward either end; posterior end rounded; lateral longitudinal welts feebly developed; prothorax with lateral swellings. Anus terminal, with a prominent posterior lip. Leg, wing and gonopod vestiges present. Thirteen differentiated somites. Body hairs short (0.05–0.11 mm.), moderately abundant and uniformly distributed; mostly with bifid tips, rarely with the branches subdivided; without alveolus or articular membrane. Integument of ventral surface of thorax sparsely spinulose, the spinules minute and in short rows. Cranium subcircular in anterior view. Head hairs moderately numerous; short (0.054–0.072 mm.); bifid tips, rarely with the branches subdivided; alveolus and articular membrane present. Antennae mounted on low convexities; drumlin-shaped; each with three sensilla.

Labrum bilobed due to an incision of the ventral border; breadth (at base) nearly twice the length; not narrowed ventrally; ventral corners rounded; anterior surface of each lobe with four or five hairs and with eight sensilla on and near the ventral border; posterior surface spinulose, the spinules minute and in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; posterior surface with about eight scattered sensilla on each lobe. Mandibles moderately sclerotized, robust and roughly quadrangular in anterior view; breadth (at base) nearly equal to length; mesal border convex; lateral border obtusely angulate near the middle; wedge-shaped, with the edge medial; distal sixth forming a distinct, slender, smooth, round-pointed apical tooth; mesal border denticulate near the base of the tooth; anterior and posterior surface roughened with numerous sublongitudinal ridges. Maxillae swollen ventrolaterally, apex conoidal, directed medially; spinulose; palp a skewed peg bearing two apical, two subapical and one lateral sensilla: galea digitiform, bearing two apical sensilla. Labium with the anterior and lateral surfaces spinulose, the spinules minute and in short transverse rows; palp a short peg, bearing four apical and one lateral sensilla; opening of sericteries wide and salient with two conspicuous projections. Hypopharynx densely spinulose, the spinules minute and in numerous subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: ten larvae from New York.)

Subgenus **Formica** Linnaeus

Cranium subheptagonal in anterior view. Mandibles with the mesal border denticulate near the base of the apical tooth.

Formica altipetens Wheeler

(Pl. IV, figs. 1–5)

Body stout; thorax and abdominal somite I curved ventrally, rest of abdomen straight; diameter greatest at the fourth abdominal somite, diminishing gradually toward either end; posterior end rounded; lateral longitudinal welts feebly developed; prothorax with a pair of lateral

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EXPLANATION OF PLATE IV

Formica altipetens Wheeler, Figs. 1–5. 1, head in anterior view, ×57; 2, typical body hair, ×185; 3, two body hairs with denticulate branches, ×185; 4, right mandible in anterior view, ×138; 5, larva in side view, ×16.

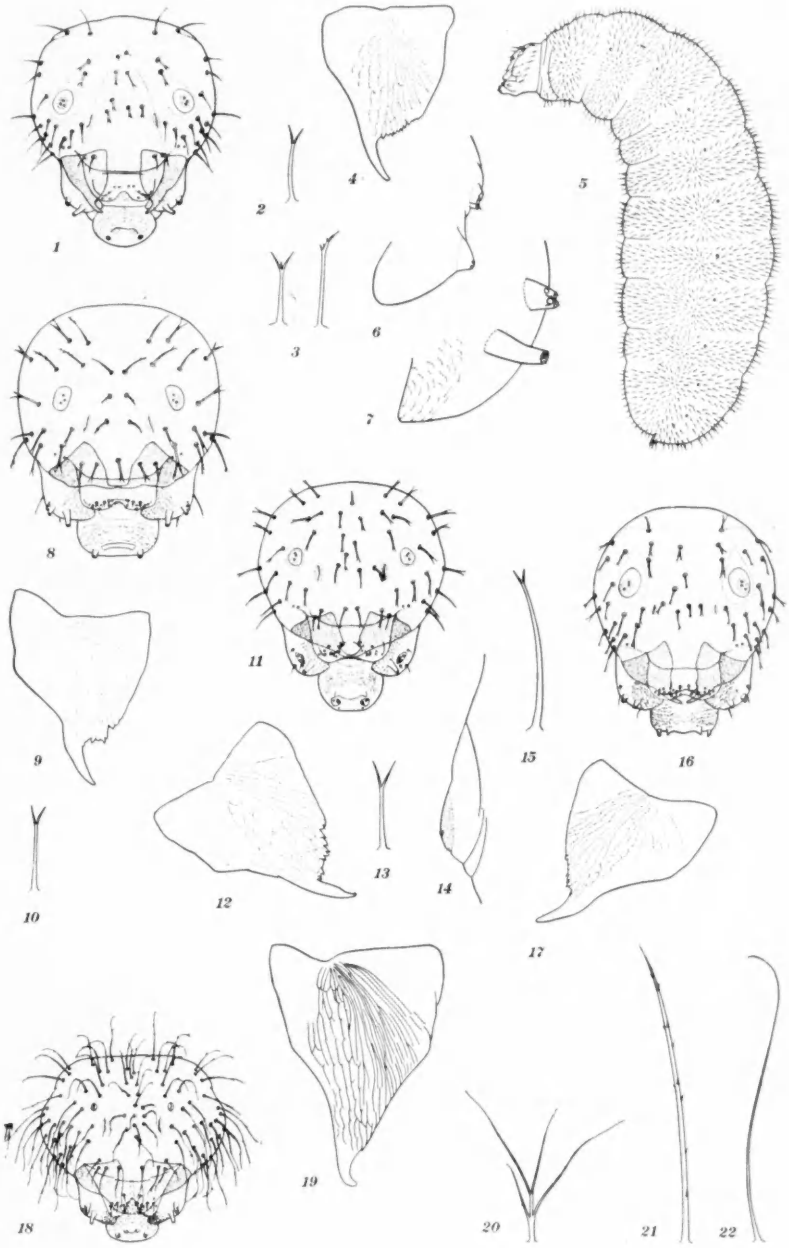
Formica neoclara Emery, Figs. 6 and 7. 6, left maxilla of very young larva in anterior view, ×235; 7, left maxilla of mature larva in anterior view, ×235.

Formica (Proformica) neogagates Emery, Figs. 8–10. 8, head in anterior view, ×67; 9, right mandible in anterior view, ×185; 10, body hair, ×185.

Formica (Raptiformica) bradleyi Wheeler, Figs. 11–14. 11, head in anterior view, ×58; 12, right mandible in anterior view, ×185; 13, body hair, ×185; 14, left antenna in side view, ×242.

Formica (Neoformica) pallidefulva nitidiventris Emery, Figs. 15–17. 15, body hair, ×235; 16, head in anterior view, ×56; 17, left mandible in anterior view, ×138.

Gigantiops destructor (Fabricius), Figs. 18–22. 18, head in anterior view, ×28; 19, right mandible in anterior view, ×95; 20–22, three body hairs, ×95.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swellings. Anus terminal, with a prominent posterior lip. Leg vestiges present. Ten differentiated somites. Body hairs moderately numerous and uniformly distributed; short (0.045–0.072 mm.); straight or slightly curved; the tips bifid with the branches frequently denticulate; without alveolus and articular membrane. Integument spinulose, the spinules minute and arranged in short transverse rows. Cranium subheptagonal in anterior view, slightly broader than long. Head hairs moderately numerous: short (0.036–0.072 mm.); simple or with the tips bifid; with alveolus and articular membrane. Antennae small, drumlin-shaped, mounted on a low convexity, each with three sensilla. Labrum small; bilobed due to a wide deep incision of the ventral border: breadth (at base) twice the length: narrowed ventrally; ventral corners rounded; anterior surface of each lobe with a ventrolateral swelling and with seven or eight sensilla and/or minute hairs; posterior surface spinulose, the spinules minute and in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; posterior surface with about 10 scattered sensilla on each lobe: ventral border with a few spinules. Mandibles moderately sclerotized; breadth (at base) four-fifths the length; roughly quadrangular in anterior view; mesal border strongly convex; lateral border obtusely angulate near the middle; wedge-shaped, with the edge medial; apical tooth smooth, long, slender, round-pointed and slightly curved medially, mesal border denticulate near the base of the apical tooth; anterior and posterior surfaces roughened with rather numerous longitudinal ridges. Maxillae rather small; slightly swollen ventrolaterally; apex conoidal and directed medially; apex spinulose, the spinules minute and in short arcuate rows; palp a skewed peg bearing one apical and four subapical sensilla; galea digitiform, bearing two apical sensilla. Labium with anterior and lateral surfaces spinulose, the spinules minute and in short transverse rows; palp a low knob, with five sensilla; opening of sericteries wide and salient with two projections. Hypopharynx densely spinulose, the spinules minute and in numerous subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: several larvae from North Dakota.)

Formica cinerea Mayr

Gantes, 1949:—"*Larve âgée* ♂, ♀ (5e stade):—Elle est d'un blanc laiteux et mesure 6 mm.; le corps est cylindrique, légèrement arqué à la hauteur du premier segment abdominal, de sorte que la tête est repliée sur le ventre; le dos est convexe, la face ventrale concave. Le bout de l'abdomen est légèrement rétréci et arrondi; l'anus est subterminal et au fond d'un entonnoir. La tête est fine et nettement plus étroite que le prothorax. Le corps comprend onze segments séparés par de profondes constrictions: il y a trois segments thoraciques et huit abdominaux. Le corps est couvert de poils, pas très serrés, raides, se bifurquant en deux branches fines: ils mesurent 0 mm. 091; les branches secondaires peuvent se diviser et on a ainsi une fourche à trois branches. Il y a également des poils simples de la même longueur. Il y a dix paires de stigmates. La tête, plus étroite que le corps, 0 mm. 5, est en forme de poire; elle est plus large dans la partie postérieure, de

beaucoup la plus importante en étendue, que dans la partie antérieure qui comprend les pièces buccales. Elle est légèrement plus haute, 0 mm. 59, que large, 0 mm. 50. La partie postérieure est creusée d'une dépression peu profonde en son milieu qui descend jusqu'au labre. Elle est couverte de poils: trente pour chaque moitié (droite ou gauche), identiques à ceux du corps. Les antennes, à la partie la plus large, forment un mamelon à peine marqué, très large, et qui porte trois sensilles à soie. Les pièces buccales sont bien différenciées. Elles comprennent: le labre ou lèvre supérieure; les mandibules, à cuticle rigide; les maxilles, portant deux palpes sensoriels chacune; le labium ou lèvre inférieure, portant deux palpes sensoreils et où aboutit l'orifice des glandes salivaires. Le labre s'avance au-dessus des mandibules. Il comprend deux lobes égaux, séparés par une échancrure profonde qui laisse voir la pointe des mandibules. Vers le bord antérieur, ventralement, et sur chaque lobe, on a un groupe de cinq sensilles à soies. Dorsalement, deux minuscules poils se trouvent sur le bord antérieur. Toute la face interne est de plus tapissée de petites soies disposées en rangées transversales. Les maxilles, de part et d'autre du labre,sont proéminentes et portent deux palpes. Le palpe distal en forme de cône, haut et mince, mesure 0 mm. 06 de long et se termine par deux sensilles à soies courtes et arrondies. Le palpe proximal est plus court et plus massif, 0 mm. 03; il porte à son extrémité un groupe de trois sensilles et sur les côtés, diamétralement opposées, deux sensilles sans soies, six poils, dont deux minuscules entre les palpes, sont clairsemés sur les maxilles. Les mandibules sont des pyramides de 0 mm. 17 de haut. Elles ont une base très large et se terminent par une pointe fine, plus foncée. La partie externe est convexe et présente trois bosses. La partie interne est concave jusqu'à la base de la pointe, puis elle est convexe et sur cette dernière partie se trouve la zone masticatrice: des dents émoussées la garnissent; elles forment de rangées qui vont en s'atténuant vers la base. Les mandibules s'insèrent profondement dans la tête par toute leur base; à la hauteur de l'insertion, on voit des lames chitineuses striées, qui vont se rejoindre dans le fond de la bouche pour former l'épipharynx. Le labium, très proéminent, apparaît tout entier sous le labre. Il porte des palpes qui sont de chaque côté de l'orifice salivaire. Ces palpes forment chacun un mamelon garni de cinq sensilles à soie. Autour de chaque palpe on trouve quatre minuscules poils. Plus à l'intérieur, le labium se continue par l'hypopharynx, qui est tapissé de petits poils formant des rangées transversales.

"b) *Larve au premier stade:* Elle mesure 1 mm., est translucide, et l'on voit par transparence les ganglions nerveux, le tube digestif et même les glandes labiales sur certaines larves. Seuls les segments thoraciques sont bien séparés; ils sont plus étroits que la tête d'un côté et l'abdomen de l'autre; ce dernier est légèrement renflé et se trouve convexe sur tout son pourtour. Le corps est légèrement arqué. On compte 11 ganglions nerveux en ne tenant pas compte des ganglions cérébroïdes et sous-oesophagiens, et 10 paires de stigmates (larve holopneustique). La tête et le thorax sont couverts par quelques poils simples; le reste du corps est nu. On retrouve sur la tête les pièces buccales, mais moins accentuées que chez la larve âgée: les palpes sont

de légères saillies translucides. Les mandibules sont de petits triangles de 0 mm. 069 de long, presque transparents. Les maxilles sont rejetées latéralement" (pp. 74–76). Pl. I shows mature and newly hatched larvae in side view, head in anterior view, hairs, mandible, antenna, galea and palps. Growth data are given on p. 86.

Krausse, 1929, pp. 102–104:—Life cycle, egg 21 days (April 10–May 1), larva 14 days (May 1–15), pupa 26 days (May 15–June 10).

Formica difficilis Emery

Apparently similar to *altipetens*. (Material studied: damaged integuments of the anterior halves of seven larvae from New York.)

Formica exsecta Nylander

This species and its subspecies ***pressilabris*** Nylander are listed as hosts of the chrysomelid larva, *Clytra quadripunctata* by Skwarra (1927, p. 84); see under *F. rufa*.

Formica exsectoides Forel

Haviland, 1947, p. 413:—In artificial nests with the temperature held at 70° F., the life cycle was: egg 10–27 days, larva 21–53 days, pupa 25–30 days; averages, 19.4, 37.1 and 26.25 days respectively. At temperatures varying from 48° F. to 94° F. the life cycle was: egg 11–54 days, larva 11–53 days, pupa 22–35 days; averages, 21, 18.2 and 27.3 days respectively. The larvae are described as curved, legless and white.

Peirson, 1923, Pl. VI*E:* larva in side view.

Formica fusca Linnaeus

Similar to *altipetens* except for the following details: Body hairs about 40 per cent more numerous and somewhat longer (0.05–0.11 mm.). Cranium transversely subelliptical; breadth 1.4 X the length. Labial palp a short peg bearing five sensilla. (Material studies: several larvae from North Dakota.)

Young larva:—Length 2 mm. Abdomen stouter and shorter than in the mature larva; head relatively larger. Thirteen differentiated somites. Body hairs shorter (0.006–0.054 mm.); less abundant on the thorax and on abdominal somites I–III; about half as numerous on the fourth somite and very few on somites V–X. Integument of abdominal somites VIII–X spinulose, the spinules minute and in short transverse rows. Mandibles narrowed at the base; apical tooth sharp-pointed and directed medially. Maxillary palp and galea shorter and stouter. Labial palp a very low frustum bearing five sensilla; opening of sericteries represented by two low conoids. An older larva (length 3.8 mm.) is similar to the mature larva.

A colony of *F. fusca* collected by W. E. LaBerge near Park River, North Dakota, June 30, 1950, includes six semipupae each of which contains a large maggot. The semipupae are enclosed in cocoons and the mecomium has been voided. Mr. Willis W. Wirth has examined one of the maggots and has informed us that it is a phorid, but that further identification is impossible.

De Geer, 1778, Pl. XLII, fig. 13:—A larva in side view, probably *F. fusca.*

Donisthorpe, 1927*b*, p. 51:—The histerid beetle *Hetaerius ferrugineus* 01. feeds on the larvae of this ant.

Eidmann, 1929:—Semidiagrammatic drawing of all the larvae of an incipient colony on nine different days between February 22 and March 30 (Fig. 2 on p. 103). Cannibalism is discussed (p. 108) and two small larvae are shown feeding on a larger larva (Fig. 3 on p. 107). Life cycle (pp. 107–108): egg 28 days, larva (until start of spinning) 17 days, larva (start of spinning until pupation) 18 days, pupa 27 days.

Eidmann, 1943, pp. 243–244:—This ant hibernates without larvae.

Fielde, 1905, p. 375:—Photograph showing semipupae (cited as *F. subsericea*). (Repeated by Wheeler, 1910, Fig. 49 on p. 84 and by Emery, 1915, Fig. 3.)

Gösswald (1934/5, p. 133):—"*Atemeles* lebt als Larve im *Formica*-Nest und frisst hier die Brut ihrer Wirte."

Formica fusca japonica Motschoulsky

Clausen (1941, p. 57) has listed this ant as a host of *Eucharis scutellaris* Gahan in Chosen; presumably the eucharid larvae are parasitoid on the ant larvae.

Formica gagates Latreille

Skwarra (1927, p. 84) listed this ant as a host of *Clytra quadripunctata:* see under *F. rufa.*

Formica neoclara Emery

(Pl. IV, figs. 6 and 7)

Very similar to *altipetens* but differing in the following details: body and head hairs somewhat longer; anterior surface of labrum with four hairs and eight sensilla on each lobe. (Material studied: numerous larvae from North Dakota.)

Young larvae (1.9 mm. long) with nine sharply differentiated somites which are hairy; the rest naked. Antennae flat and not mounted on an elevation. Mandibles narrowed slightly at the base. Maxillae with the apex paraboloidal; palp a low elevation bearing five sensilla; galea a low subcone, with two apical sensilla.

Formica neorufibarbis algida Wheeler

Worker larva similar to *altipetens.* (Material studied: 17 larvae from Michigan.) A queen larva of this subspecies from a New Hampshire colony is very similar to the worker larva except for larger body size, relatively smaller head and sparser body hairs which are simple spikes about 0.054 mm. long.

Formica obscuripes Forel

Similar to *altipetens* but differing in the following details: Body hairs slightly longer. Anterior surface of labrum with two hairs and about eight sensilla on each lobe; posterior surface with about six

sensilla on each lobe. (Material studied: numerous larvae from North Dakota.)

Weber (1935, p. 190) has given the life cycle as: egg 23–53 days, larva 7–33 days, worker pupa 31–93 days.

Formica rufa Linnaeus

Adlerz (1886, p. 56):—Internal anatomy.

Bedel, 1895:—*Eucharis bedeli* Cameron "attaque les cocons de *Formica rufa* L." in Bohemia. Presumably the eucharid larva is parasitoid on the ant larva. Rushka (1924, p. 88) suspected, however, that the hymenopteron was *E. ascendens* Fab. Wasmann (1894, p. 168) refers to *Chalcura* sp. bred from cocoons of this ant in "Prag (Polak)."

De Geer, 1778, Pl. XLI, Figs. 16 and 17:—Larva in side view.

Dewitz, 1878, pp. 78–79:—"Die erwachsenen Arbeiterlarven. . . . besitzen eine Länge von 0.006 m.; ihr Körper besteht aus 13 Ringen ausser dem Kopfe und spitzt sich nach vorn etwas zu, während das hinters halbkuglig abgerundete Ende fast noch denselben Durchmesser zeigt, wie der mittlere, dickste Theil. Kopf und Brust krümmen sich der Bauchseite zu. Der Kopf ist . . . klein, doch nimmt man deutlich die Kiefer und Unterlippe mit ihren Tastern wahr. Die Länge der ersten Körpersegmente ist auf der Rückenseite eine viel beträchtlichere als auf der Bauchseite, und so wird die Krümmung des vorderen Abschnittes hervorgebracht. Die Stigmen sind kreisrund und liegen, der Rückenseite genähert an dem vordern Theile eines jeden Segmentes; das erste Stigma gehört, wie man sich aufs deutlichste überzeugen kann, dem zweiten Brustringe an. Wenngleich bei der späteren Entwickelung die Theile des Brustkastens sich sehr verändern, und die Stigmen sich hierbei verschieben, so dass das erste auf der Grenze des ersten und zweiten Brustringes zu liegen kommt, und man bei dem erwachsenen Thier nicht mehr unterscheiden kann, welchem abschnitte der Brust es angehört, so lehrt uns doch das Larvenstadium, dass das erste Segment stigmenfrei ist.—Die noch nicht erwachsenen Larven besitzen dieselbe Körpergestalt, doch in den jüngsten Stadien einen im Verhältnis viel stärkeren Kopf."

Donisthorpe, 1915, Pl. III = 1927*a*, Pl. III:—An excellent photograph of a larva in side view.

Donisthorpe, 1927*b*, p. 55:—The histerid beetle *Myrmetes piceus* Pk. feeds on the ant larvae.

Eidmann, 1943, pp. 244–250:—This species hibernates without larvae.

Pérez, 1902:—His description of the internal anatomy of this larva was followed by Wheeler (1910, pp. 75–76 and Fig. 44 on p. 78).

Ratzeburg, 1832:—"Die Larve . . . ist milchweiss, überall gleichmässig schwach durchscheinend und fein und ziemlich dicht behaart. Sie besteht: 1) aus zwölf fast gleich gebildeten, häutigen, sehr weichen, ziemlich breiten Ringen, deren jeder aus zwei Theilen besteht, einem oberen gewölbteren, und einem unteren flacheren. Die Einschnitte, wo beide rechts und links sich vereinigen, liegen auf jeder Seite der Bauchseite, so dass der obere Theil grösser als der untere ist. Der letzte Ring ist sehr klein, stumpf kegelförmig und hat am Ende eine Falte, hinter welcher der After liegt. Die Luftlöcher (*stigmata*) liegen

am Obertheil jedes Ringes, zur Seite desselben. Es findet sich an den Ringen weder von Füssen noch von Wülsten eine Spur; 2) aus einem kleinen, fast kugelrunden dunkler gefärbten und härteren Theil, welcher, an den ersten Leibesring sich anschliesst und Kopftheil genannt werden kann, aber keinesweges Kopf heissen darf, wofür er bisher von den Schriftstellern gehalten wurde. Er sieht einem, freilich nur sehr kleinen, Kopfe allerdings sehr ähnlich, denn er ist völlig unabhängig von der zwölf Leibesringen, bewegt sich ganz frei und kann sich sogar in den ersten Ring wie in eine Kappe zurückziehen; man sieht dann an der Unterhälfte des letztern eine halbmondförmige Falte entstehen, welche dem Ausschnitt an der Unterseite des Bienen- und Ameisenkopfes ähnelt, in den sich die innern Mundtheile befestigen. Auf der Oberseite dieses Kopftheils bemerkt man nun weder Augen . . . noch Antennen, was diejenige, die ihn für einen wahren Kopf ansprechen, doch schon hätte bedenklich machen sollen; man bemerkt nur jederseits eine etwas gewölbte, in der Mitte mit einem kleinen Eindruck versehene fast hornige Hälfte (Hülle für die künftig sich bildenden Oberkiefer), und zwischen beiden, in der Mittellinie, einen erhabenen, etwas glänzenden, nach vorn sich erweiternden Streif. Am vordersten Ende trägt eine jede hornige Hälfte ein kleines dreieckiges, spitziges, dunkelbraunes, glänzendes festes Hornstückchen, die eigentlichen Oberkiefer, *mandibulae* der Larve, welche man das lebende Thier auch bewegen sehen kann. Unterhalb dieser liegen die innern Mundtheile, welche so zart, weiss und gallertartig sind, dass man bei der angestrengtesten Beobachtung mit der Lupe doch irren kann. Da ich sie einigemale auf verschiedene Weise gebildet gesehen zu haben glaube, so vermuthe ich, dass sie schon in diesem ersten Stadium einer Verwandlung unterliegen, dass sie sich in einer frühen Zeit, man möchte sagen auf einer Stufe befinden, auf der die Bienenlarven, in Hinsicht der Mundtheile sehr lange verweilen. Während nämlich bei der ganz jungen Ameisenlarve alle innern Mundtheile in einen fast kegelförmigen, überall gleichmässig gallertartigen Theil verschmolzen waren, der nur an der Seite nach vorn eine schwache Ausrandung zeigte, so sah ich später diesen Theil immer nur getrennt in zwei deutliche, durch Absätze und Bewegungen geschiedene Theile. Der Theil vor den Mandibeln erschien breit abgerundet-viereckig, vorn mit einer Ausrandung und zu jeder Seite derselben mit zwei borstenartigen, braunen Spitzen, deren beide innere aber so nahe an dem mittelsten Theil standen, dass man sie auch für diesem zugehörig halten konnte. Der eben genannte mittelste Theil steht wieder unterhalb des vorigen, ragt aber etwas über ihn hinaus. Er ist vorn gerade abgestutzt und scheint walzenförmig zu seyn. Er ist beweglich und das lebende Thier kann ihn zurückziehen und wieder etwas vorstrecken. In einer Mittelstufe zwischen dieser und der nächsten sah ich deutlich den durch die weisse, gallertartige Masse braun durchschimmerden Oesophagus in diesen Theil münden. Auf der Unterseite des Kopftheils sieht man die beiden zuletzt genannten Theile einen für sich bestehenden, etwas gewölbten Theil bilden" (pp. 149–153). The semipupa was described on p. 156. Fig. 1, larva in side view; Fig. 2, larva in ventral view; Figs. 3 and 4, head in anterior view; Fig. 5, head in posterior view; Fig. 6, larva in dorsal view; Fig. 7, semipupa in side view; Fig. 8, anterior end of semipupa in side view.

Skwarra (1927) concluded concerning the larvae of the chrysomelid beetle *Clytra quadripunctata* L. "dass ihre Nahrung in erster Linie in der Brut der Ameisen, besonders Larven und Puppen, besteht. Sie sind also nicht harmlose Mitbewohner der Ameisennester, die sich vom Abfall ernähren, sonder gefährliche Bruträuber" (p. 95). *F. rufa* is listed as a host (p. 83).

Formica rufa pratensis Retzius

Gösswald (1932, p. 38 and 1934/5, p. 142) recorded *Eucharis ascendens* F. reared from queen pupae in Germany; presumably the eucharid larvae had been parasitoid on the ant larvae.

Skwarra (1927, p. 84) listed this subspecies as a host of *Clytra quadripunctata:* see under *F. rufa* above.

Formica ulkei Emery

Similar to *altipetens* but differing in the following details: Body hairs sparse. Anterior surface of labrum with four hairs and about six sensilla on each lobe. Maxillary palp a short forked peg with an apical sensillum on each fork and with three lateral sensilla. (Material studied: numerous larvae from North Dakota.)

The queen larva differs from that of the worker in the much larger body, the relatively smaller head, and in the hairs which are few, slender, whip-like and about 0.13 mm. long.

Park, 1929, p. 205:—The carabid beetle, *Tachyura incurva* (Say) has "been seen to devour crushed larvae and pupae." In 1935 (p. 223) he reported it as feeding on the brood in laboratory nests.

Formica uralensis Ruzsky

Skwarra (1927, p. 84) listed this species as a host of *Clytra quadripunctata:* see under *F. rufa* above.

Subgenus **Raptiformica** Forel

Cranium transversely subelliptical in anterior view. Mandibles with the mesal border jagged near the base of the apical tooth.

Formica (Raptiformica) bradleyi Wheeler

(Pl. IV, figs. 11–14)

Body stout; thorax and abdominal somite I curved ventrally, rest of abdomen straight; diameter greatest at the fourth abdominal somite, diminishing gradually toward either end; posterior end narrowly rounded; lateral longitudinal welts feebly developed; prothorax with a pair of lateral swellings. Anus terminal with a prominent posterior lip. Leg, wing and gonopod vestiges present. Thirteen differentiated somites. Body hairs short (0.05–0.09 mm.), moderately abundant and uniformly distributed, mostly with tips bifid, rarely trifid or simple; without alveolus or articular membrane. Integument spinulose, the spinules minute and in short transverse rows. Cranium transversely subelliptical in anterior view, a third broader than long. Head hairs

moderately numerous, short (0.045–0.063 mm.); with the tips bifid or simple; alveolus and articular membrane present. Antennae mounted on low convexities; drumlin-shaped; three sensilla each. Labrum bilobed due to a wide shallow impression of the ventral border; about twice as broad (at base) as long; slightly narrowed ventrally; ventral corners rounded; anterior surface of each lobe with a ventrolateral swelling and with a dozen sensilla and/or minute hairs; ventral border spinulose; posterior surface spinulose, the spinules minute and in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; posterior surface of each lobe with six scattered sensilla. Mandibles rather small and moderately sclerotized; breadth (at base) nearly equal to length; roughly quadrangular in anterior view; mesal border convex; lateral border obtusely angulate near the middle; wedge-shaped, with the edge medial; apical tooth distinct, slender, smooth, tapering, round-pointed and slightly curved medially; mesal border jagged near the base of the apical tooth; anterior and posterior surfaces roughened with numerous sublongitudinal ridges. Maxillae swollen ventrolaterally; apex short-conoidal and directed medially; apex spinulose, the spinules minute and in short rows; palp a stout skewed peg bearing five sensilla; galea digitiform, bearing two apical sensilla. Labium with anterior and lateral surfaces spinulose, the spinules minute and arranged in short arcuate subtransverse rows; palp a low knob bearing five sensilla; opening of sericteries wide and salient with two projections. Hypopharynx densely spinulose, the spinules minute and in numerous subtransverse rows, the rows grouped in two subtriangles which have their bases near the middle. (Material studied: numerous larvae from North Dakota.)

Formica (Raptiformica) sanguinea Latreille

Donisthorpe, 1927*b*:—The staphylinid larva *Lomechusa strumosa* F. devours the brood of this ant (p. 22). Another staphylinid (*Dinarda pygmaea* Wasm.) was seen to devour a larva (p. 28). The histerid beetle *Hetaerius ferrugineus* Ol. feeds upon the larvae and pupae (p. 51). Referring to the staphylinid genus *Lamprinus*, "both the adult beetle and their larvae devour the ants' eggs, larvae, and pupae" (p. 72).

Gösswald, 1932, p. 38 and 1934/5, p. 142:—*Eucharis ascendens* F. was reared from queen pupae of this ant; presumably the eucharid larvae were parasitoid on the ant larvae.

Gösswald (1934/5, p. 127) and Skwarra (1927, p. 84) have listed this ant as a host of *Clytra quadripunctata:* see under *F. rufa*.

Wheeler, 1928a:—The larvae of *Lomechusa* "devour the brood and are also fed by regurgitation. . . . The ants seem to prefer the predatory larvae to their own, or perhaps regard them as unusually promising ant larvae. In consequence of this infatuation the Lomechusa larvae often destroy the greater part of the brood, so that in *sanguinea* colonies heavily infested with the parasites, the queen larvae develop abnormally" (p. 207) into peudogynes (p. 208). (See also p. 262.) (=Wheeler, 1926, pp. 250–252 and 315–316.) (Brief reference by Gösswald, 1934/5, p. 126.)

Formica (Raptiformica) sanguinea subnuda Emery

Similar, in general, to ***bradleyi*** but with longer hairs on the anterior surface of the labrum, with the mandibles slightly more elongate and with the apical tooth slightly sharper. (Material studied: numerous larvae from North Dakota.)

Tribe **Gigantiopini** Ashmead

Wheeler (1922b, pp. 190–191) used larval (in addition to adult) characters to justify the removal of *Gigantiops* from "Forel's tribe Oecophyllini and to provide an independent tribe for its accommodation." "When we compare *Gigantiops* with *Oecophylla* we are struck at once by the great differences in the structure of the larva, pupa and adult and in habits. . . . The larva of *Gigantiops* is like that of *Camponotus*, but very different from that of *Oecophylla*, and the pupa is enclosed in a cocoon."

Genus **Gigantiops** Roger

Thorax forming a short thick neck, which is strongly arched ventrally; abdomen straight, swollen and subcylindrical. Body hairs abundant, rather short and of three types: (1) simple, slender and whip-like, (2) 2- to 4-branched, (3) moderately stout, slightly curved and denticulate. Cranium transversely subelliptical in anterior view; integument sparsely spinulose. Antennae minute. Head hairs numerous, long, denticulate and whip-like. Labrum with a median longitudinal furrow on the anterior surface. Mandibles heavily sclerotized. Maxillary palp finger-like. Labial palp a skewed peg.

Wheeler, 1922*b*: see above under the tribe.

Gigantiops destructor (Fabricius)

(Pl. IV, figs. 18–22)

Thorax forming a short thick neck, which is strongly arched ventrally; abdomen straight, swollen and subcylindrical. Posterior end rounded. Leg, wing and gonopod vestiges present. Seven or eight differentiated somites. Body furnished with a dense and uniform covering of rather short hairs or three types: (1) simple, slender, and whip-like, 0.21–0.49 mm. long; (2) 2- to 4-branched, 0.07–0.21 mm. long; and (3) moderately stout, slightly curved, denticulate, with long or short side branches, 0.14–0.23 mm. long. Body hairs without alveolus and articular membrane. Integument densely spinulose, the spinules minute and arranged in subtransverse rows. Cranium nearly 1.5 × as broad as long, genae bulging, occipital border nearly straight, dorsal corners broadly rounded; integument spinulose, spinules minute and in short transverse rows. Head hairs numerous, long (0.16–0.32 mm.), whip-like and denticulate; with alveolus and articular membrane. Antennae minute, each with three sensilla. Labrum twice as broad (at base) as long; strongly narrowed ventrally, conspicuously bilobed due to a deep median incision of the ventral border, which is continued onto the anterior surface as a median trench; anterior surface of each lobe with five or six short hairs and two or three sensilla;

five sensilla on (or near) the ventral border of each lobe; posterior surface spinulose, spinules minute to relatively long and in rows which radiate from the dorsolateral angles, the rows continuous near the base but broken distally; about a dozen sensilla scattered irregularly over the posterior surface of each lobe. Mandibles heavily sclerotized; subtriangular in anterior view; wedge-shaped, with the edge medial; apex forming a short, smooth, rather stout, round-pointed tooth which is curved medially; anterior and posterior surfaces roughened with numerous longitudinal ridges. Maxillae with the apex paraboloidal and roughened with numerous minute isolated spinules; palp finger-like, with two apical, two subapical and one lateral sensilla; galea finger-like, with two apical sensilla. Labium with the anterior and lateral surfaces spinulose, the spinules minute and in short transverse rows near the middle but longer and in arcuate rows laterally; palp a skewed peg bearing one apical, three subapical and one lateral sensilla; opening of sericteries wide and salient, with two projections. Hypopharynx spinulose, the spinules minute and arranged in subtransverse rows, the rows grouped in two subtriangles whose bases are near the middle. (Material studied: six damaged integuments from British Guiana.)

Wheeler, 1922*b*:—"As soon as I began to dig into their nest the workers leaped out and made off, holding their larvae in their mandibles" (p. 189). See also above under the tribe.

A COURSE IN THE USE OF THE ELECTRON MICROSCOPE

The annual Cornell Summer Laboratory Course in Techniques and Applications of the Electron Microscope will be given this summer from June 15 to June 27, 1953, by our laboratory of Electron Microscopy in the Department of Engineering Physics. The course under the direction of Dr. Benjamin M. Siegel will have Dr. James Hillier of the RCA Laboratories, Princeton, New Jersey, and Dr. C. E. Hall of M.I.T., Cambridge, Mass., as guest lecturers this year.

The course is designed for those research workers, institutional and industrial, who have recently entered the field of electron microscopy or who are now planning to undertake research problems involving applications of this instrument. Further inquiries should be addressed to Dr. Benjamin M. Siegel, Department of Engineering Physics, Rockefeller Hall, Cornell University, Ithaca, New York.

OBITUARIES

DR. MELVILLE THURSTON COOK

The death of Dr. MELVILLE THURSTON COOK in Hyattsville, Maryland, on August 11, 1952, marked the passing of a pioneer in more than one field of botanical and agricultural science. Dr. Cook was born on September 20, 1869 in Coffeen, Illinois. He was widely schooled and the recipient of several degrees. He was granted the bachelor of arts degree in 1894 at Stanford University, where he studied under the noted Dr. David Starr Jordan. He received his Master of Arts degree from De Pauw in 1902 and in 1904 the Doctor of Philosophy degree from Ohio State University. In 1940, Dr. Cook received the honorary Doctor of Science degrees from both the University of Puerto Rico and De Pauw University.

Dr. Cook possessed an active mind and his interests extended much beyond the fields of his specific interests of mycology and plant pathology. In the field of entomology, and a member of the Entomological Society of America, he contributed a number of technical papers on insect galls and gall insects and the transmission of plant viruses.

His varied experience included: professor of biology at De Pauw University from 1897–1904; plant pathologist, Central Agronomy Station, Santiago de las Vegas, Cuba, 1904–1906; plant pathologist, New Jersey Agricultural Experiment Station, 1907–1911; professor of botany at Rutgers University, 1911–1923; and from 1923 to 1940, he was plant pathologist, and at times, director of the Insular Experiment Station at Rio Piedras, Puerto Rico. From 1942 to 1951, he was "visiting professor" at Louisiana State University.

His dominant characteristic was an untiring and persistent will to work and an uncompromising and unyielding persistence in the pursuit of his cherished work. The many friends and co-workers of Dr. Cook will long remember him as one who could smile through shadow and sunshine, and one who was always willing to help, and one whose loyalty to his chosen field remained steadfast to the end.—ERWIN L. LECLERG

CHARLES ORRIS ESSELBAUGH

CHARLES ORRIS ESSELBAUGH, a member of the Entomological Society of America since 1943, was born near Fostoria, Ohio, on November 26, 1898. He was educated in a rural Ohio grade school, in the Fostoria High School, in Ohio State University where he was graduated with the degrees Batchelor of Science in Agriculture in 1923 and Master of Science in 1926, and in the University of Illinois where he received the degree of Doctor of Philosophy in 1945. On May 28, 1927 he married Nettie V. Craddock, who became his close companion in his work and hobbies and who survives him. He died peacefully during the night, at the height of his career and without a preceding illness, at Minot, North Dakota, on June 17, 1952.

Dr. Esselbaugh's career was a varied one. His earlier professional life was spent as a teacher in the Ohio high schools. Since 1930 he has been engaged in work as an entomologist for the Ohio Agricultural Experiment Station, the Shell Oil Company, and the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture. His projects have dealt with the European corn borer and the Oriental fruit moth in Indiana, white pine blister rust in Ohio, Dutch elm disease in New Jersey, pear psylla in Washington, range grasshoppers in Montana and Wyoming, and wheat stem sawfly in North Dakota. In 1948 he and his coworkers on the Black Fly Investigations project in Alaska amassed a collection of nearly 19,000 insects (excluding mosquitoes and black flies) and related arthropods, probably the largest ever assembled from that area.

His research, aside from assigned projects, has been chiefly on the bionomics and taxonomy of the Pentatomidae. He described one new species, *Chlorochroa*

opuntiae, and his contribution to our knowledge of the immature forms and biology of this family is considerable. Publication began late in his life, but then became constant and substantial. He left in his papers one almost-completed major work and notes which were obviously intended to form the basis for several additional papers. The following list of publications which appeared during his life time will be supplemented by probably two posthumous works, one of which, in co-authorship with Kathryn Sommerman and Reece I. Sailer, will deal with the Alaskan black fly studies.

1945. Biology of the Pentatomidae (Hemiptera). Pp. 1–8. Abstract of a thesis. Urbana, Illinois.
1946. A study of the eggs of the Pentatomidae (Hemiptera). Ann. Ent. Soc. Amer. 39: 667–691.
1947. Some notes on the biology of *Hymenarcys aequalis* Say (Pentatomidae). Bul. Brooklyn Ent. Soc. 42: 25–30.
1947. Some remarks on the genus *Chlorochroa* (Hemiptera, Pentatomidae) and a new species. Bul. Brooklyn Ent. Soc. 42: 164–169.
1949. Notes on the bionomics of some midwestern Pentatomidae. Ent. Amer. 28: 1–73.
1949. A bionomic note on the taxonomic status of the form *pyrrhocerus* of *Euschistus tristigmus* Say (Hemiptera, Pentatomidae). Proc. Ent. Soc. Washington, 51: 160–163.

—M. T. J.

NATHAN BANKS

With great regret I inform you of the death of Prof. Nathan Banks, at Holliston, Massachusetts, on January 24th, 1953, at the age of 84 years. He was born at Roslyn, N. Y., April 13th, 1868. He received a B.S. degree from Cornell University in 1889 and an M.S. from the same university in 1890. He was employed by the Division of Entomology, U. S. Department of Agriculture, from 1890–1916. From 1916–1944 he was Curator of Insects at the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, and from 1928–1935 he was also Associate Professor of Zoölogy at Harvard. He held both his Harvard titles emeritus after his retirement. He was one of the best-known entomologists of his time. He published extensively on Neuroptera and on other orders of insects and also on spiders, and he built up and maintained in the Museum of Comparative Zoölogy one of the finest collections of insects in America. He is noted also for his bibliographical work with the literature of insects. We, his associates at the Museum of Comparative Zoölogy, feel his loss very deeply.

(Signed) P. J. Darlington, Jr.

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